Adaptation to elevation in Brassicaceae species of the central Alps

Inauguraldissertation

zur

Erlangung der Würde eines Doktors der Philosophie

vorgelegt der

Philosophisch-Naturwissenschaftlichen Fakultät

der Universität Basel

von

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Basel, 2021

Genehmigt von der Philosophisch-Naturwissenschaftlichen Fakultät

auf Antrag von

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Basel, den 15 Dezember 2020

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TABLE OF CONTENTS

SUMMARY

Species are restricted in their spatial distribution, but the reasons behind this phenomenon are still not entirely known. Temperature has been considered to play an important role for a long time, for example because of the commonly observed overlap between isoclines and distribution limits, or for the direct impact that temperature has on the physiology of organisms. From an evolutionary point of view however, it is unclear why the climate niche of species does not seem to evolve such that species ranges can extend unlimitedly. To shed light on the evolutionary constraints limiting species distribution, I studied patterns of adaptation along an elevational gradient, which is essentially a thermal gradient. I chose a macro-evolutionary approach and included in my analyses 100 Brassicaceae species covering a high diversity of restricted elevational ranges in the European Alps. Species were compared in their thermal responses and thermal adaptation based on a climate chamber experiment and a transplant experiment on a mountain slope, with 5 transplant sites from 600 to 2000 m of elevation. Climate chamber experiments revealed that low- and high-elevation species mainly differed in the response of growth to temperature, with high-elevation species being better at growing when daily temperatures reached a high maximum, but worse at growing to large size when night frosts occurred. Therefore, results indicated a trade-off between fast growth under warm conditions and frost tolerance. Analyses on an association between elevational range size and phenotypic plasticity revealed no support for a positive link. However, I found that increased thermal heterogeneity selected for stronger thermal specialisation, countering the hypothesis that temporal environmental variability selects for increased plasticity. The transplant experiment demonstrated that species were indeed adapted to their optimal elevation of occurrence; lifetime performance declined if the transplant site was at a different elevation than the typical elevation of occurrence of a species. Patterns established not via temperature-dependent mortality, but because reproduction declined with increasing difference in elevation relative to the typical elevation. The probability of fruit set decreased with increasing distance. Furthermore, I found that reproduction negatively

affected survival to the next year, suggesting an allocation trade-off between reproduction and longevity that may be also important in constraining the climate niche and its evolution. Overall, this body of work supported that elevational range limits generally reflect niche limits, and that species seem to have been selected for thermal specialisation. Evolutionary constraints in the widening of the climate niche seem to include genetic trade-offs in growing fast under warm conditions and being frost tolerant, and an allocation trade-off between reproduction and longevity. It is these two axes of trade-offs or four axes of life-history aspects that future micro-evolutionary studies should focus on to confirm their role in constraining the evolution of the climate niche within species.

ACKNOWLEDGEMENT

First, I want to thank and express my sincere gratitude to my supervisor Yvonne Willi, for allowing me to undertake this adventure and for her continued support and patience over the years.

I also want to thank PD Dr. Günter Hoch, PD Dr. Josh Van Buskirk and Prof. Dr. Markus Koch for being part of my thesis committee and for their helpful advice, as well as Prof. Dr. Jake Alexander who accepted the role of the outside evaluator of this thesis.

Many thanks to all the colleagues and friends I met at the University of Basel for their help, discussions, and good time we had together: Georg Armbruster – "the expert", Olivier Bachmann, Janisse Deluigi, Jens Paulsen, Susanna Riedl, Markus Funk, Antoine Perrier, Dario Sánchez-Castro, Franziska Grob, Kay Lucek, Selim Bouaouina, Theofania-Sotiria Patsiou, Sylvia Martinez, Hannah Augustijnen, Jessica Heblack and Judith Schepers. Furthermore, I would like to thank the many students who helped with the measurements and contributed to this grand data set I could base my research chapters on.

Thanks to all those who have ventured to Calanda, sharing fate under the most diverse and adverse conditions, and lightening the sleepless days.

Last but not least, a big thank-you goes to my family: my grandparents, my parents and my sister, as well as my beloved Michela, for their support and tolerance while I wrote this thesis and in life in general.

GENERAL INTRODUCTION

Species have spatially restricted distributions. Some species are limited to a few square-kilometres while others occur on most of the globe. However, none of them occurs everywhere. This fact has fascinated biologists over the past centuries, leading to many contributions on the causes of restricted ranges, including in recent years. Biogeographers proposed that dispersal mediates the distribution of species (Wallace 1880), with historical biogeography mainly focusing on the interplay between dispersal and vicariance; uninhabitable territory can act as a barrier if dispersal distances are shorter, and consequently they limit the species to cross them (Croizat 1952). Examples of barriers are mountain ranges or big water bodies such as oceans for terrestrial species. Important geographical barriers were also produced by climatic oscillations such as Quaternary glaciation cycles, which are known to influence the distribution of many extant species to the very day (Hewitt 2000). Nonetheless, some important contemporary phenomena, including anthropogenic climate warming, demonstrate that colonization of new areas is possible, suggesting that further reasons for restricted ranges must exist.

In addition to biogeographers, ecologists and evolutionary biologists started taking charge of this fundamental biological question (MacArthur, 1972; Gaston 2003; Connallon and Sgrò 2018; Willi and Van Buskirk 2019). To understand range limits, ecologist work with the concept of the niche. As early as 1917, Grinnell introduced the idea that ecological properties of a species describe its ecological niche, which is related to where in space a species can be found. The idea was then developed further by Hutchinson (Hutchinson 1957), who defined the concepts of the fundamental and realized niche. The fundamental niche refers to the abiotic conditions and resources needed by a species to maintain viable populations. The realized niche is the part of the fundamental niche from which a species is not excluded by interactions with others. While the niche is not a place on earth, a species should occur only where niche conditions are generally met. In recent years, evidence has

accumulated that the geographic distribution of species is linked with niche limits (Pulliam 2000; Lee-Yaw et al. 2016). Furthermore, evidence has accumulated that while the niche of species may be affected by many variables, larger limits in spatial distribution can often be explained well by climate alone (MacArthur, 1972; Lee-Yaw et al. 2016).

Thermal isotherms have been found to coincide with species geographic limits (Salisbury 1926; Iversen 1944; Dahl 1951; Root 1988), which suggests a key-role of temperature among the components of the climatic niche. Across the globe, temperature shows variation from the equator to the pole, with a decrease of 0.73 K in mean annual temperature for each degree in latitude, or decrease of 1 K with a shift northward of 154 km. But apart from this general trend, also considerable variation exists. For example, the decrease in the warmest month is smaller, and patterns are not as strong in the southern hemisphere (i.e., -0.48 K and -0.57 K; Frenne et al. 2013). Thermal variation also occurs with similar magnitude along elevational gradients, but over much shorter distances. With an increase in elevation, the atmospheric temperature declines on average by 0.6 K per 100 m worldwide (i.e., 1 K with a shift upwards of 166 m; Körner 2003). This turnover in temperature has been shown to be associated with a turnover in species occurrence (Brown et al. 1996; Bryant et al. 2008).

The observed macro-climatic variation in the environment is also associated with noticeable geographical patterns in morphological traits as recognized and summarised by some ecogeographical rules. Allen's rule (Allen 1877) stands for the relationship between surface-area-to-volume ratio that varies with environmental temperature. Bergmann's rule (Bergmann 1848) suggests that larger size correlates with colder environments. Finally, Gloger's rule (Gloger 1833) states that more pigmented species are more likely to occur near the equator. Those widespread relationships between environment and morphological traits are another type of evidence for the tight link between species occurrence and climate. This is not surprising as temperature is known to affect biochemical reaction rates (Kingsolver 2009) and as a consequence the physiology and performance of organisms

(Pigott and Huntley 1981; Angilletta 2009; Sakai and Larcher 2012). Thermo-biologists identified convergence in thermal adaptation (both as tolerance or resistance) and latitudinal variation in animals (Sunday et al. 2012, 2019). In line, experiments in which species were cultivated outside of their range showed often reduced fitness or an increase in mortality (e.g. Hargreaves et al. 2014). Summing up, strong evidence indicates a key-role of the ecology of the species on determining its range.

There is an evolutionary angle to range limits. Wallace (1880) already suggested the important role of evolutionary processes to restricted ranges, and as pointed out by Caughley et al. (1988), the explanation of distribution limits must consider physiological adaptation. The evolutionary view is that the absence of a species is affected by a lack of adaptation of the niche (Mayr 1969). Comparisons of species on a macro-evolutionary scale have revealed that large numbers of traits evolved slowly in the past (Simpson 1944; Freckleton et al. 2002; Estes and Arnold 2007), which suggests that niche evolution is constrained. Consequently, although macro-scale adaptation to abiotic conditions seems at the base of range expansion, important questions remain. The central one is: What constrains niche evolution within individual species? Additionally, on a finer scale, environmental heterogeneity in the landscape make the picture even more complex. For example, at higher elevation, micro-climate can dramatically change over a few meters, allowing plants growing at 2000m to experience similar thermal environments as plants growing at 1000m. This calls for a need of studying thermal-adaptation on a micro-climatic level.

Studying limits to thermal adaptation should not be merely an academic exercise. Climate change has always affected species occurrence but these days, anthropogenic effects accentuate thermal variation, and thermal adaptation is crucial for the longer-term persistence of species under climate warming. This is particularly crucial at the current warm-edge of species distributions. Knowing in what way the climatic niche is constraining current distribution and the extent to which thermal adaptation is needed for coping with increasing temperature and altered precipitation patterns

is of fundamental relevance to applied sciences, such as conservation, ecosystem functioning, forestry and crop production.

The aim of my PhD was to investigate the extent to which thermal adaptation can explain elevational range-limits within a common evolutionary context: the environment (i.e. the Alps) and across multiple species within the same family (i.e., phylogenetic). And, I wanted to find out what the causes of constraints could be.

In **Chapter 1** I focused on the traits of adaptation that systematically differ among species with different elevational ranges. One-hundred Brassicaceae plants species from the central Alps were raised in controlled environments under three different temperature regimes and phenotyped for several eco-physiological traits. Traits were analysed in search of a signature of divergent adaptive evolution and genetic trade-offs.

The extent to which thermal-plasticity contributes to range-size was the main question of **Chapter 2**, where for all the traits assessed in Chapter 1, a plasticity index was calculated and then correlated with geographic and thermal-environmental descriptors of range-size. Again, the focus was on differences among species explaining their distribution, but also on potentially limiting factors.

Chapter 3 and **Chapter 4** were based on transplant experiments to test plant responses under natural thermal conditions. Specifically, in **Chapter 3** I studied whether species are optimally adapted to climatic conditions typical for their elevational range and what the main aspects of the temperature were that restricted them. Here 30 Brassicaceae species were raised under 5 common gardens located from 600 to 2000 m. Then I tested whether components of overall performance (growth, survival, and reproduction) varied along the climatic gradient depending on the elevational distribution of species and what the aspects of the thermal regime were that constrained performance most. Finally,

Chapter 4 focused on reproductive events, phenology, and their consequences for overall performance and the thermal players.

The study system

Alpine ecosystems cover 3% of all land area and are characterized by a reduction of 0.6 K per 100 m in elevation. Because of this steep climatic gradient over elevation, high mountain areas such as the Alps are an ideal place to study the evolution of the climatic niche on a macro-evolutionary scale. Within this gradient, it is possible to encounter habitats of Mediterranean thermophiles and habitats of arctic species. The European Alps are characterized by strong winds, increase in precipitation and a shortening of the growing season with elevation (Körner 2003).

In the central European Alps, there are approximately 180 species of Brassicaceae of which 28 are strictly high-elevatoin species. They occur in a variety of disturbed habitats (e.g., exposed rocks), but they are never dominant, suggesting a strong role of climatic factors in niche differentiation. On a global scale, Brassicaceae is a worldwide, non-mycorrhizal Angiosperms family with about 3'700 species (including important agricultural cultivars) subdivided into 3 main lineages (Lineage I, II and III, Al-Shehbaz et al. 2006). Cruciferous plants have also been investigated for various aspects e.g., stress tolerance, morphology, biogeography, and evolution, and current knowledge on gene function of flowering plants comes from studies of the model plant *Arabidopsis thaliana* (L.) Heynh. (Meinke et al. 1998), making this family an excellent system for both comparative and evolutionary studies (Franzke et al. 2011).

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CHAPTER 1

Trait divergence and trade-offs among Brassicaceae species differing in elevational distribution

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SUBMITTED IN EVOLUTION

Acknowledgements

We thank Lea Bona, Camilla Jenny, Adrian Möhl, Ramon Müller, Jens Paulsen, Florian Schreier, and Daniel Slodowicz, for collecting seeds in the field. Georg Ambruster, Olivier Bachmann, Markus Funk, Kay Lucek, Michela Meier, Jens Paulsen, Theofania-Sotiria Patsiou, Antoine Perrier, Susanna Riedl, Dario Sanchez-Castro, Martinez Sylvia and Nora Walden, helped with sowing seeds, taking plant measures and fruitful discussions. Finally, we would like to thank all the field botanists that contributed to the collection of occurrence data for the InfoFlora database.

ABSTRACT

Species have restricted geographic distributions and the causes are still largely unknown. Temperature has long been associated with distribution limits, suggesting that there are ubiquitous constraints to the evolution of the climate niche. Here we investigated the traits involved in such constraints by macroevolutionary comparisons involving around 100 Brassicaceae species differing in elevational distribution. Plants were grown under three temperature treatments (regular frost, mild, regular heat) and phenotyped for a set of phenological, morphological and thermal resistance traits. We tested distinct models of trait evolution with elevation of species as a predictor, while correlative approaches identified trade-offs across traits. Analyses pinpointed speed of growth under heat and frost tolerance as the most discriminating traits between high- and low- elevation species, with high-elevation species being fast-growing under heat but less frost-tolerant. Evolutionary models supported adaptive divergence for both traits, while correlation analysis indicated their involvement in a moderate trade-off. Furthermore, unequal potential for trait evolution was discovered under the three thermal regimes, with evolvability across traits being 36% more constrained under mild or heat conditions compared to regular frost. Overall, results suggest that trade-offs between traits under adaptive divergence contribute to the disparate distribution of species along the elevational gradient.

Key words: heat and frost stress – macroevolution - Ornstein-Uhlenbeck - phylogenetic signal - range limits - thermal niche

INTRODUCTION

Species have restricted geographic distributions, but what the causes behind this phenomenon are is an old and still unsolved question in both ecology (MacArthur 1972; Gaston 2003) and evolutionary biology (Connallon and Sgrò 2018; Willi and Van Buskirk 2019). From an ecological point of view, range limits reflect limits of the ecological niche, where the niche is defined as the abiotic and biotic conditions that allow a species to persist (i.e., the realized niche *sensu* Hutchinson 1957; Leibold 1995). From an evolutionary point of view, range limits reflect limits to niche evolution. But why is it that species fail to adapt to environmental conditions beyond their current range? MacArthur (1972) suggested that a possible reason is exclusive divergent adaptation across habitats. He envisioned that specialization to one environment imposes high demographic costs under colonization of a new environment, or in other words, a trade-off. Trade-offs are a key concept in evolution, likely affecting all aspects of ecological specialization *vs.* generalization (Rosenzweig 1995) and including species distribution limits, but they have been rarely studied in this context.

Among the many factors that may affect the persistence of organisms, climate is known to be critical in controlling large-scale distribution (MacArthur 1972). Temperature affects any biochemical reaction rate (e.g., Kingsolver 2009), together with the physiology of organisms, their growth, survival and reproductive performance (Pigott and Huntley 1981; Angilletta 2009; Sakai and Larcher 2012). For these reasons, environmental temperature has long been seen as critical in determining the distribution of species. Furthermore, many past studies noticed coincidences between geographic distribution limits and temperature isotherms (Salisbury 1926; Iversen 1944; Dahl 1951; Root 1988). More recently, the field of species distribution modelling confirmed the good agreement between range limits and climate variables (e.g., Normand et al. 2009; Lee-Yaw et al. 2016). Further studies looked into phenotypic patterns associated with the most limiting aspects of climate at range limits, particularly at the cold end of distribution. Loehle (1998) suggested that the northern range limit of North American tree species was determined by cold tolerance. Phenotypic data supported

that species from higher latitudes were usually more tolerant to the cold than those from lower latitudes (Addo-Bediako et al. 2000; Hawkins et al. 2014; Wen et al. 2018; Sunday et al. 2019). Similarly, abiotic stress appeared to be linked with the upper elevational range limit for some mountainous plant species suggesting a predominant role of negative temperatures (Vetaas 2002; Macek et al. 2009; Körner et al. 2016). For the warm end of distribution, the prevailing hypothesis for range limits emphasized the importance of negative species interactions (MacArthur, 1972; Gaston 2003; Louthan et al. 2015). However, there is no clear evidence that e.g., competition explains the southern range limit of species at a global scale; some studies supported the hypothesis (Loehle 1998, Pither 2003), while others did not (Cahill et al. 2014). Probably because of the general dismissal of climate as a factor determining warm-end limits, few studies focused on how organisms cope with heat in the context of species distribution limits (e.g., Sunday et al. 2012; Kellermann et al. 2012;), particularly in plants (e.g., Kappen 1981; Wos and Willi 2015).

What are the sources of constraints in the evolution of the climate niche? According to simple evolutionary principles, genetic variation and selection are needed for a response to selection and adaptation (Falconer and Mackay 1996). Genetic constraints may involve low genetic variation of traits under selection. However, microevolutionary studies have shown that there is commonly ample genetic variation in single traits and strong natural selection acting on populations (Mousseau & Roff 1987, Houle 1992, Kingsolver & Diamond 2011), raising the expectation of rapid and ubiquitous adaptation through highly evolvable and selection-sensitive traits. Another type of genetic constraint is trade-offs in fitness-relevant traits, often seen as an obstacle to adaptive evolution limiting the rate of evolution (Futuyama and Moreno 1988; Bennett and Lenski 2007; Walker 2007). Negative genetic correlations among traits (from the fitness' point of view) appear mainly due to two non-exclusive causes. The first is that both the environment and the genetics of traits exert a limitation on trait values through differential allocation of limited amounts of resources (Bell 1984; van Noordwijk and de Jong 1986). The second cause is purely genetic; pleiotropic antagonism occurs when an allele

increases the fitness via a first trait but reduces it via a second (Rose 1983). If we translate this in a thermobiology context, it is reasonable to assert that thermal extremes impose selection on some traits, resulting in a better thermal performance under one type of extreme, paid at the price of its reduction in performance in a contrasting environment or a contrasting aspect of the biology of the species. In ectothermic animals, relatively common trade-offs involve thermal resistance on the one hand, and growth, starvation resistance, longevity or reproduction on the other hand (Luckinbill 1998; Norry and Loeschcke 2002; Hoffmann et al. 2005; Stoks and De Block 2011; Casanueva et al. 2012), or cold and heat tolerance (Norry et al. 2007). Temperature can also mediate trade-offs between traits, e.g., between lifespan and reproduction (Mockett and Sohal 2006), or longevity and body size (Norry and Loeschcke 2002); or reversing the sign of the correlation (reviewed in Sgrò and Hoffmann 2004). In plants, trade-offs were discovered between cold tolerance and frost resistance (e.g., *Raphanus raphanistrum*; Agrawal *et al.* 2004), and between speed of development and frost tolerance (Koehler et al. 2012; Molina-Montenegro et al. 2012; Bucher et al. 2019).

While micro-evolutionary studies can shed-light on trade-offs, those involving traits related to the climate niche have not revealed any cohesive pattern (e.g., Williams et al. 2012; Kelly et al. 2013). However, in the last decades, the field of comparative phylogenetics has developed macro-evolutionary models that allow the study of the adaptive co-evolution of traits while accounting for shared history of the species (summarized in Garamszegi 2014). Based on comparative models, the phylogenetic signal of traits can be estimated and interpreted in the context of niche conservatism (Cooper et al. 2010). Furthermore, the contribution of different evolutionary processes and constraints to respond to selection can be inferred (Butler and King 2004). Three evolutionary processes are typically modelled. A first is *genetic drift*, by which inherited characters slowly change in random direction and accumulate differences over time. The process is modelled by Brownian motion (BM). A second process is *stabilizing selection*, a likely result of dependencies among co-adapted characters opposing to external selection (Wagner and Schwenk 2000). It is modelled by Ornstein-Uhlenbeck

(OU1) diffusion, which constrains BM toward an optimal trait value. Recent improvements allow variation in the direction of OU diffusion across lineages, depicting the third process of *divergent selection* (OUM, Beaulieu et al. 2012). In the context of climate niche evolution, the comparison among these models was applied to study associations between the climate niche and life forms in high-alpine *Androsacae* plants (Boucher et al. 2012), longevity and niche breadth in the Eriogonoideae (Kostikova et al. 2013) or between abiotic disturbance and life-history in *Leucadendron* (Tonnabel et al. 2018). In animals, the approach was used to study niche evolution in turtles (Rodrigues et al. 2018), the evolution of life-histories in Parulidae (Gómez et al. 2016), and habitat specialization in lizards (Blom et al. 2016) and clown fish (Litsios et al. 2014). Examples emphasize the great potential the methods have in detecting traits of adaptation to climate and revealing potential trade-offs in such adaptation.

Here we studied trait divergence associated with the predominant elevational distribution of plant species and analysed trait data for patterns of trade-offs, all in a macroevolutionary context. Elevational gradients are promising in the context for at least two reasons. On the one hand, elevation provides a steep climatic gradient in most mountainous regions, where over a short geographic distance a reduction of the mean temperature of 0.5K every 100 m of elevation is found rather consistently (Körner 2003). On the other hand, species often occupy narrow elevational ranges (Körner 2003), making elevational gradients unique systems for studying adaptation to thermal stress and constraints in such evolution. Our study involved 100 Brassicaceae species occurring in the central Alps of Europe, with median elevational occurrence varying from 400 to 2800 m a.s.l. Seeds of the species were raised in climate chambers under three different temperature regimes (regular frost, mild, regular heat), and twenty eco-physiological traits related to coping with thermal extremes, to life-history, competitive ability and resource use were measured. Four main hypotheses were tested. (i) Species differ in trait expression depending on their elevational distribution. (ii) Traits differ in the signature of past evolutionary processes having acted on them. (iii) Phylogenetic conservatism

in traits depends on the growth environment. And (iv) there are trade-offs among traits associated with adaptation to elevation.

MATERIAL AND METHODS

Plant species

One hundred taxa (i.e., species and subspecies) belonging to the Brassicaceae family and naturally occurring in the Swiss Alps from the colline to the alpine life zone were selected. Apart from a good representation of the elevational gradient, other criteria were level of ploidy (diploid taxa preferred) and good representation of the phylogeny (list in Supplementary material A1). In the general area, around 180 species of Brassicaceae occur, of which 28 are strictly high-elevation species. On a global scale, Brassicaceae is a worldwide angiosperm family composed of 3'700 species (including important agricultural members) subdivided into three main lineages (Al-Shehbaz et al. 2006).

For this study, seeds were collected from March to September during the years 2015-2017 at two different sites for each species in the Swiss Alps. The sites were around the most common elevation for each species, at least 50 km apart from each other and preferentially from different biogeographic regions. For plants with very restricted distributions, only one population was sampled, but the number of individuals was doubled. At each site seeds were collected from 10 to 30 different mother plants. At a site, they were collected over an area of usually 50 m^2 and spaced out from each other by 5 m. For endangered species on the Red List 2002 for Switzerland (Moser et al. 2002), authorization for sampling was obtained by the respective Cantonal authority. Sampled seeds were stored in paper bags (80 g m^{-2}, 60 × 90 / 12 mm, ELCO AG, Brugg, Switzerland) under cold (4 °C), dark and dry (added silica gel) conditions until sowing.

Raising of plants under three growth treatments

Design - The experimental design involved the raising of 100 taxa, each represented by 2 populations and 3 seed families per population, i.e. 6 seed families per species. Plants of each maternal line were raised under 3 temperature treatments, and used as biological replicates within species, accounting for intraspecific variation. The experiment was split into 6 blocks, with a different seed family per species in each block, and each block contained the 3 temperature treatments (regular frost, mild, regular heat). The final design resulted in 1'800 individuals (100 taxa × 6 maternal lines each in a different block × 3 treatments = 1'800 individuals). Maternal lines within population were selected randomly and seeds of a maternal line haphazardly. We performed the experiment twice: once by not treating seeds (S1) and once by treating seeds with gibberellic acid (GA_3) (S2).

First sowing (S1) - Seeds were germinated in climate chambers under controlled conditions in October 2017. Seeds were sown in multipot-trays (0.06 L, 54 pots per tray Ø 4.4 cm, BK Qualipot; gvz-rossat.ch, Otelfingen, Switzerland). Each pot was filled with a mix of soil (bark compost, peat and perlite, Aussaat- und Pikiererde; Oekohum, oekohum.ch, Herrenhof, Switzerland) and sand (0-4mm) in a ratio of 2:1. Three seeds of a family were sown in the same pot to ensure to have at least one seedling per pot. Seeds were not covered by soil, but trays were covered by a garden fleece (windhager.eu, Hünenberg, Switzerland). Then seeds were stratified for 3 weeks in dark and cold (~5-7 °C constant), and afterwards they were transferred to growth chambers (MobyLux GroBanks, CLF Plant Climatics, plantclimatics.de, Wertingen, Deutschland). Growth chambers were located inside a PlantMaster (CLF, Plant Climatics, plantclimatics.de, Wertingen, Deutschland) with managed humidity and temperature. Trays were kept at 18 °C during daytime (8 h) and 15 °C during night-time (16 h), at 75% relative humidity (RH), and a light intensity of 150 µmol m^{-2} s^{-1} (fluorescent white lamps and red-LED). Blocks were randomly assigned to growth chambers, and twice a week, blocks were moved to a different chamber, with re-randomized positioning. When cumulative

germination reached at least 40% and no additional increase was scored, excess germinated seedlings were used to fill pots with no germination with the following priority: use of same maternal line within block or the same population or the same species. In the 7th week after the end of stratification, the temperature treatment started. Plants were moved in a greenhouse with similar conditions as in the GroBanks. Control plants stayed there constantly, while frost-treated plants were transferred in a climate chamber overnight for treatment (Climecab 1400, Kälte 3000 AG, Landquart, Switzerland) and heat-treated plants were transferred to climate chambers from mid-morning to mid-afternoon.

Second sowing (S2) - Seeds were germinated in climate chambers under controlled conditions in February 2018, with similar conditions as described above. Two seeds of each family were placed in a 1.5 ml eppendorf tube and filled with 500 µl of GA_3 solution (500 ppm, Merck KGeA, Dornstadt, Germany). Seeds were stratified for 1 week in dark and cold (4 °C constant; Climecab 1400). After this period, seeds were sown in multipot-trays and transferred to growth chambers. After 3 weeks, excess seedlings were used to fill pots with no germination. In week 4, germinated plants were moved in climate chambers and were subjected to three temperature treatments.

Treatment - The three temperature treatments were: "frost" (F), "mild/control" (M) and "heat" (H). Frost: 20 °C (day), then -2 °C for 1 h (-4.8 K h^{-1}; night) and back to 20 °C (+7.3 K h^{-1}; night). Mild/control: 20 °C constant. Heat, S1: 20 °C (beginning of day), then 42 °C for 1 h (+5.5 K h^{-1}; day), back to 20 °C (-8.3 K h^{-1}; day), 20 °C (night). Heat, S2: 20 °C (beginning of day), then 40 °C for 1 h (+5 K h^{-1}; day), back to 20 °C (-8.3 K h^{-1}; day), 20 °C (night). Plants within the S1 heat treatment experienced some drought stress during treatment, and therefore temperature during the heat peak was reduced by 2 °C in S2 to eliminate this problem. All treatments were conducted at 12:12 h light:dark and a light intensity of about 300 µmol m^{-2} s^{-1} (S1: MH-lamps in greenhouse, S2: LED white lamp) and 75% RH. Plants were acclimated to treatment conditions two days before the beginning of treatment by exposing them to milder extremes, 2 °C for the frost treatment, and 35 °C

for the heat treatment. We selected extreme temperatures based on records in the field during the vegetative period (Larcher andWagner 1976; Sutinen et al. 2001; Körner 2003), while for mild condition we used a standard control value. Trays were randomized daily within each block, while blocks where moved to a different climate chamber twice a week (S2). Plants were kept under these conditions until the 14th week after sowing (S1) and the 9th week after sowing (S2). At the end of the experiment when trait assessments were performed, mean species number across traits within treatment ranged from 53 (heat) to 75 (mild) in S1 (N = 970), and from 83 (frost/heat) to 86 (mild) in S2 (N = 1406). Across the treatments and rounds of sowing, 93 of the 100 taxa were represented as some never germinated.

Trait assessment

Seed size (SSIZ) - For all the species, 10-20 seeds per field-collected maternal plant were haphazardly selected. When possible, the same seed families were used as for sowing; if not enough seeds were available, another maternal seed family was randomly picked. Seeds were then photographed under a stereomicroscope (Leica M205 C, Leica Microsystems GmbH, Wetzlar, Germany) and the area of each seed measured (in mm^2) with the image analysis software ImageJ v.1.44 (Schneider et al. 2012).

Time to germination (TGER) - After stratification, seeds were checked for germination daily during the first week and every other day until the beginning of treatments. Germination was defined as when two cotyledons were fully open. Time to germination was adjusted for the mid-point of checking for germination, when cotyledons were observed a first time and previous checking.

Growth (IGR, MGR, XMID, ASYM, NLEA) - Plant growth was measured once a week for 5 weeks, starting the week before the temperature treatment began. The two longest leaves of every plant were measured. Leaves with more than 25% damage or senescence were not considered. Means across leaves were used to estimate the growth trajectory by fitting seven alternative growth models

(linear, exponential, power, two-, three-parameter logistic, Gompertz and Bertalanaffy). Models were fit in R v.3.6.1 (R Core Team 2013). The three-parameter logistic model produced the best fit with the data based on weighted AIC. Parameters extracted from the model were: asymptotic size (ASYM), maximal growth rate (MGR, i.e., $scale^{-1}$) and the time to fastest growth (XMID). The traits of XMID was multiplied by '-1' such that higher values reflected faster growth (indicated by the abbreviations (-)XMID). In order to identify the initial growth rate (IGR), we used the 'maxcurve' function {soilphysics} (da Silva and de Lima. 2017) to locate the knee in the exponential phase of the curve and calculate the derivate with the 'deriv' function. In the S2 experiment, the number of leaves was additionally counted once a week. Only few species reached a final asymptote and therefore the number of leaves on day 35 of treatment was used in analysis (NLEA).

Leaf functional traits (SLA, LDMC, LA, LDI, LTh) - During week 8 of treatment, 1-2 fully elongated leaves from the 2nd to 3rd whorl were harvested from each plant and used for leaf trait assessment. For very tiny leaves (<25 mm^2) twice the amount of material was collected. Leaves were immediately weighed individually on microbalances (AT250, XA205 DualRange, Mettler Toledo, Columbus, USA) to the nearest 0.01mg. Leaves were then scanned (CanonScan, LiDe120, Canon, Tokyo, Japan) and analysed by ImageJ to obtain leaf area (LA, in mm^2) and perimeter (in mm). Leaves were finally packed in paper bags and dried at 60 °C for 72 h in an oven (Termaks AS, Bergen, Norway), and then weighed again using the same balance. Specific leaf area was calculated as area over dry weight (SLA, in $mm^2\ mg^{-1}$) and leaf-dry-matter content as the ratio of dry weight over fresh weight (LDMC, in mg g^{-1}). Leaf dissection index (LDI) was calculated as the ration between perimeter and area following Fourier's transformation (Kincaid and Schneider 1983). Traits were measured on individual leaves and the plant mean value was used for data analyses. In S2, leaf thickness was additionally estimated using a mini-digital thickness gauge (digitalmicrometers.co.uk) (LTh, in mm).

Frost and heat resistance (electrolyte leakage, RES) - During week 9 of treatment, 3 healthy and fully developed leaves from the 3rd to 5th whorl were picked and a circular disc of 6mm diameter punched out on the tip of the blade, avoiding main nervures. Each leaf disc was placed in a 15 ml falcon tube (Sarstedt, PP, 120x17 mm, Nümbrecht, Germany) filled with 2 ml of dH_2O and kept in there for 0.5-1 h to wash the sample. The water was discarded, and the leaf in each tube was exposed to short thermal stress. Based on a pilot study and reports in the literature (e.g., Levitt 1980; Kappen 1981; Gauslaa 1984), the temperatures of -12 °C and -6 °C (S1), and -10 °C and -5 °C (S2) were chosen to assess frost resistance, and +47 °C and +52 °C (S1), and +45 °C and +50 °C (S2) to assess heat resistance. Only acclimated plants were used in S1 (plants pre-exposed to frost for assessing frost resistance, and plants pre-exposed to heat for assessing heat resistance), while plants of the mild growth treatment were also subjected to all of the selected stress temperatures in S2. Frost exposure was applied by first filling tubes into aluminium boxes (to buffer thermal variation), which were then placed in programmable freezers, one per negative temperature. After an initial 0.5 h at 5 °C for temperature equilibration, the target temperature was approached with a cooling rate of -3 K h^{-1}. Samples were kept at the target temperature for 1 h, and then temperature was increased to +5 °C. Heat exposure was done in a water-bath (Julabo TW20, HuberLab, Aesch, Switzerland) by submersing tubes for 5 min in the bath for temperature equilibration. Then tubes were kept in the bath for 1 h, in dark. After frost and heat exposure, all tubes received 3 ml of dH_2O and were stored overnight in dark and at room temperature for electrolytes to dissolve in the water. Electrolyte concentration was measured with a calibrated conductivity meter (Fe30/EL30, Mettler Toledo, Columbus, USA). Then tubes were sealed and subjected to a boiling bath for 1 h. Tubes were again kept overnight and total leakage was measured on the following day. Electrolyte leakage due to stress was calculated as the ratio of conductivity measured after stress to conductivity after the boiling bath, in per cent. Resistance was calculated by the formula: 100% - electrolyte leakage, with higher values indicating higher resistance.

Frost and heat tolerance (TOL) - Tolerance to repeated frost or heat during the growth phase was calculated as a growth parameter (MGR, (-)XMID, ASYM) in the frost or heat treatment minus the estimate in the mild treatment, divided by the estimate in the mild treatment (relative measure of tolerance). All terms were first calculated on a population level (mean across all replicates of a population-treatment combination). Analyses of tolerance were based on species means (mean of populations within species). We used the term frost/heat tolerance *sensu lato* (*s.l.*) to generally refer to tolerance and resistance together.

All analyses were performed on species mean trait values revealed in a particular growth treatment, based on population means.

Statistical analysis

Trait expression differing with temperature treatment during growth and elevational distribution - The effect of growth treatment, median elevation of species distribution, and their interaction on traits was tested using generalised linear mixed models based on Markov Chain Monte Carlo techniques with the 'MCMCglmm' function of the R package MCMCglmm (Hadfield 2010). The relatedness matrix of species was considered as a random factor (ginverse option on ultrametric tree processed via 'inverseA' function). Information on species relatedness came from a phylogeny produced based on several dozen chloroplast genes (Patsiou et al. 2020) and was pruned to species included in this study with the function 'treedata' of package geiger (Harmon et al. 2008). Several trait measures were log-transformed prior to analysis in order to improve normality: SSIZ, MGR, NLEA, LA, LDI, RES(+)T2, TOL_MGR and TOL_ASYM. Species elevation was the centred value of the median of reported elevation of occurrences of a nation-wide species inventory data set (infoflora.ch). Treatment was coded as categorical variable, and contrasts were performed against "mild" condition or, for tolerance, against "frost". Finally, when a trait was assessed in the same way in the two rounds of

sowing, sowing was included as an additional (cross) random effect. Significance was calculated with the function 'mcmc.pval' of the package MCMC.OTU (Mikhail 2016) on 3 different chains with different seed number. Sampling behaviour was visually inspected, and number of iterations, burning and sampling interval adapted to each model to retain 1'000 effective sampling size. All analyses and figures were performed with the statistics software R v.3.6.1 (R Core Team 2014).

Past evolutionary forces - Phylogenetic analyses were performed to assess the contribution of evolutionary processes in shaping trait divergence among species. Analyses were run separately for the two rounds of sowing and the three temperature treatments, on mean values per species. We tested four evolutionary models using the R package mvMORPH (Clavel et al. 2015): BM, BMM with different speed for the different regimes, OU1 and OUM. For BMM and OUM, the contrasting environmental regime was elevational distribution of taxa; a binary distribution was assumed, "low" *vs.* "high" elevation. Assignment to one of the two classes was based on the book "Flora Alpina" (Aeschimann et al 2004) and in some cases corrected based on InfoFlora (infoflora.ch) distribution information. Regimes were assigned to each species and then the ancestral state reconstructed on 100 independent stochastic character maps on the phylogenetic tree with 'make.simmap' in phytools (Revell 2012). Simulations were performed on the full phylogenetic tree, using either a model of equal rate of evolutionary switch (ER) or a model of unequal rate (ARD). Simulated trees were first pruned and evolutionary models run on all the trees. Models were compared based on AICc. As OUM was often the best or second-best model, the phylogenetic half-life (i.e. the time required for a trait to evolve halfway towards its adaptive optimum) was calculated for all traits assessed in the three growth environments. A small value in half-life indicates fast adaptation to the optimum and a lack of phylogenetic inertia, while a higher value indicates that traits retain the influence of their ancestral values. We tested for an effect of growth environment on the evolutionary lability of traits with a generalised linear mixed model with MCMCglmm (as specified above). Phylogenetic half-life was cube-root transformed to improve normality, and trait was a random effect. Analysis focused on the

second round of sowing (S2), because number of species across treatments was greater and balanced, and more traits were assessed.

Multi-trait relationships and trade-offs. Trait associations with elevational distribution were tested by distance correlation using the 'dcor.test' function of the R package energy (Rizzo and Székely 2016). Significance was assessed based on 1'000 bootstrap replicates. In order to identify putative trade-offs between pairs of traits, Pearson correlation coefficients were calculated using the 'rcorr' function of the package Hmisc (Harrell 2019). Prior to correlation analysis, we estimated trait residuals after accounting for phylogeny with the function 'pgls' of the package caper (Orme et al. 2018), and the trait mean was subsequently added to residuals to facilitate interpretation. The traits of XMID was multiplied by '-1' such that higher values reflected faster growth (indicated by the abbreviations (-)XMID. To reduce the number of traits while keeping the most discriminating ones in regard to elevational distribution of species, discriminant analysis of principal components (DAPC) was performed with 'dapc' of the package adegenet (Jombart 2008). The optimal PC number to retain was selected based on α-score analysis with the function 'optim.a.score' of the package adegenet and 1'000 simulations. Traits contributing with a loading higher than 0.1 were selected and used for correlation. Discriminant analysis was performed on centered (mean = 0) values that were divided by the standard deviation. Analyses were performed only with data of the second round of sowing (S2).

RESULTS

Trait expression differing with temperature treatment during growth and elevational distribution

Results on trait expression differing between growth treatments and species depending on their elevational distribution are summarized in Table 1, Fig. 1 and Supplementary material A2. A high fraction of traits responded to the temperature treatments during growth. Under regular frost

compared to mild conditions, plants reached the time of maximal growth earlier, and they had smaller asymptotic size and fewer smaller leaves. Their leaves had more dry mass per surface area and were thicker (smaller SLA, larger LTh). However, frost resistance of leaves was not significantly different after pre-exposure to frost during growth. Under regular heat during growth compared to mild conditions, the maximal growth of plants was significantly faster, the time of maximal growth reached earlier, but asymptotic plant size was smaller. The leaves of plants were smaller under heat, thinner (larger SLA) and leaf dry matter to fresh weight was reduced (lower LDMC). Heat resistance of leaves was higher after regular heat exposure during growth, indicating heat stress acclimation. Finally, tolerance to heat was generally higher compared to tolerance to frost for both maximal growth rate and asymptotic size.

Median elevation of species distribution alone explained only significant variation in the general expression of few traits. High- compared to low-elevation species did not significantly differ in aspects of growth, but they had smaller leaves and less dry matter to fresh weight in leaves (LDMC). Furthermore high elevation species had more frost-resistant leaves after frost exposure during growth in sowing S1 but not in sowing S2, and they had more heat-resistant leaves after pre-exposure to heat in sowing S1 (T2) but less heat-resistant leaves in sowing S2, suggesting that thermal resistance of leaves is generally labile. Significant interactions between elevation of species distribution and treatment were found, but they were only significant for the heat treatment. When exposed to heat, high elevation species – compared to those with lower elevational distribution – reached maximal growth even faster, had a higher maximal growth rate, but they ended up being smaller. Or, in other words, these growth and leaf traits of high-elevation species showed an even stronger response to heat than species generally had. In line, high-elevation species had lower tolerance to heat stress compared to low-elevation species in terms of size (being smaller), but not for maximal growth; maximal growth was reached earlier and was faster. Finally, low-elevation species had more dissected leaves and high-elevation species less dissected leaves under heat.

Past evolutionary forces

Table 2 summarizes results on analyses of evolutionary processes having acted on traits, for each growth environment (for a full account see Supplementary material A3, A4). When results were qualitatively similar, only results for experiment S2 are shown; if results differed, this is indicated. First of all, with the exception of LA_{mild} and $RES(+)T1_{S1.heat}$, the two evolutionary switch models were equally well supported (i.e., 'ER', under which low and high elevation are predicted to change at equal rate; or 'ARD', under which for- and backward rates between states can take different values, Supplementary material A4). This result suggests that the best supported evolutionary models were a real description of our phylogenetic effect and not related on how the evolutionary regime had established. Apart from OUM, the other commonly best model was OU1; BMM was rarely and BM never the best model.

The two leaf traits with consistent difference between low-and high-elevation species in MCMCglmm analyses were also those for which OUM was the best model (except for leaf area under mild conditions). High elevation species had lower optima for leaf area, leaf dry matter content and dissection index. The growth parameter with consistently best support for OUM was asymptotic size, with high-elevation species having lower optima for size. What follows are traits with consistent (S1 and S2) best support of OUM but more inconsistency across growth environments. Growth rates of high-elevation species under mild conditions had lower optima but optimal time to maximal growth under heat was shorter. Leaf thickness (LTh) of high-elevation species had a higher optimum under mild conditions. Thermal tolerance traits showed hardly any consistent pattern in regard to support for OUM, maybe with one exception: tolerance in asymptotic size to frost and heat was lower for high-elevation species. Time to germination was only assessed under mild conditions, before treatments began, and the best supported model was OUM, with high-elevation species having an optimum time that was later than low-elevation species. Finally, traits expressed under heat were

more consistently associated with divergent optima, particularly in S2, when more species were assessed. Traits expressed under mild conditions were second in revealing a signature of divergent optima and divergent selection along the elevational gradient (8 out of 16 traits). Finally, only five out of 16 traits expressed under frost revealed a signature of divergent optima (31% : 50% : 69%; regular frost : mild : regular heat).

Strength of selection (*alpha*, Supplementary material A3) was highly variable depending on trait and trait-by-treatment interaction. Its values ranged between 0.06 ($ASYM_{S1.heat}$) and 2079.13 ($TGER_{S2}$). Important variation also existed for the same character measured in different treatments (e.g., in S1 $ASYM_{S1.heat}$/$ASYM_{S1.frost}$ 0.06/1.9). Strongest selection does not apply on all the treatments on the same trait. Under frost, highest alpha values were found for TOL_ASYM (alpha = 125, S1; alpha = 77, S2), while under heat, highest values were found for XMID (alpha = 86, S1; alpha = 67, S2). Measures of phylogenetic half-life (i.e., $\ln(2)\, alpha^{-1}$; Tab. 3, Supplementary material A3) were often significantly greater than 0 but the associated values commonly small (i.e., often <1 Mya, Table 3), suggesting not much phylogenetic inertia in the evolution of most traits. The most limited traits were associated with morphology and size, e.g., LDI with a half-life between 4-7 Mya, LA_{mild} with 7 Mya, ASYM with 3-11 Mya, NLEA with 4-7 Mya, and SSIZ with 8Mya. More generally, analysis on the effect of temperature during growth on the half-life of trait evolution revealed a significant reduction by 36% under frost stress compared to mild or heat conditions (i.e., traits evolve 36% faster, Supplementary material A5).

Multi-trait relationships and trade-offs

Based on a full data set, with traits assessed in the three environments being considered different traits, we analysed which trait combinations separated best high- from low-elevation species. The optimal number of principal components to retain based on α-score selection was 41 for the entire

dataset (accounting for 99% of trait variation, Fig. 2A). Such selection was able to back-assign taxa to their elevation of origin with an accuracy >95% (Fig. 2A).

Mid-point of growth under heat, (-)$XMID_{heat}$, tolerance to heat based on XMID, (-)TOL_{heat}_XMID, and tolerance to frost based on asymptotic size, TOL_{frost}_ASYM, were the traits contributing most to discriminating low- from high-elevation species in multivariate trait space (Fig. 2B). When the threshold for the loading value was lowered from 0.1 to 0.05, then initial growth rate under frost (IGR_{frost}) and leaf area under mild conditions (LA_{mild}) appeared as additional discriminating traits. Finally, trait correlations were analysed. Distance correlation was significantly different from 0 ranging from 0.32 to 0.49, supporting moderate trait association. Pearson correlation was negative and significant between frost tolerance based on asymptotic size (TOL_{frost}_ASYM) and heat tolerance based on the mid-point of growth ((-)TOL_{heat}_XMID; r = -0.29, p = 0.015), suggesting a negative trade-off between maintaining large size under frost and fast growth under warm conditions (Fig. 2C, Supplementary material A6).

DISCUSSION

Past studies in ecology and biogeography have indicated that temperature is a limiting factor of species distribution, suggesting that there are ubiquitous constraints to climate adaptation and the evolution of the climate niche. Our analysis pointed to a moderate trade-off between accelerating growth under heat and tolerance to frost in around 100 Brassicaceae species of the central Alps (summary of test results in Table 4). In line, high elevation plants were found to accelerate growth under heat and to have lower tolerance to frost, and this seemed to be favoured by divergent selection. In contrast, low-elevation species were not faster under regular occurrence of heat, but they were more frost tolerant. Results are discussed in the context of adaptive divergence patterns across the

elevational gradient, trade-offs in climate adaptation, the likely causes, and the aspects of climate that may cause divergence.

Trait differences between low- and high-elevation species

Generalized linear models and evolutionary models mainly overlapped in their prediction that species differed in trait expression depending on whether they were low- or high elevation species (Table 4). The traits that were most consistently different across the growth environments were leaf size and leaf dry matter content, with plants from higher elevation having smaller leaves with a lower ratio of dry to fresh weight (lower LDMC). Divergence in selection optima pointed in the same direction. Some recent studies on multi-species comparisons also found a reduction in leaf size with increasing elevation (Qi et al. 2014; Zhong et al. 2014), but dry-matter-content was either higher or lower (Zhong et al. 2014; Midolo et al. 2019). Studies also reported evidence for a reduction in plant height (Qi et al. 2014; Rosbakh et al. 2014), which we did not measure, a reduction in specific leaf area (Qi et al. 2014; Rosbakh et al. 2014; Midolo et al. 2019), and an increase in leaf thickness (Gratani 2014; Zhong et al. 2014; ; Thakur et al. 2019). None of the latter three traits were found to differ between low- and high-elevation species in our work or in that of others (Körner et al. 1986; Zhong et al. 2014). However, what many studies documented rather consistently was that high-elevation tree species were more frost resistant (Körner 2003; Taschler and Neuner 2004; Neuner 2014; Neuner et al. 2020; Schrieber et al. 2020). In our analysis, acclimated leaves of high-elevation species were more resistant to a frost temperature of -12 °C in one round of sowing, but not to -10 °C in a second round of sowing. Overall, high elevation plants seem to consistently share small leaves, and possibly heightened resistance to extreme frost.

Other traits differed between low- and high-elevation species, but the difference became only significant when plants were exposed to regular heat peaks. More specifically, high-elevation species

were significantly faster growing under the regular occurrence of heat, but their final size and leaf area were smaller. In line, divergent optima of selection were more common under mild and heat conditions compared to regular frost (Table 2). The result of more traits under divergent adaptation to - or within - warmer conditions was unexpected. In fact, the occupying of low-elevation habitats probably preceded the occupying of high-elevation environments over evolutionary times. Therefore, in high-compared to low-elevation species, we would have expected greater divergent adaptation to frost, but we found more evidence for divergent adaptation to warm conditions.

In contrast to the many traits we found to differ between high- and low-elevation species at least in one of the growth environments, traits found to be separating the two groups of species most – by discriminant analysis - were few. They were the time to maximal growth under heat, tolerance to heat based on maintaining fast growth, and tolerance to frost based on plant size. Plants from high elevation were faster in reaching maximal growth under heat, in general and when scaling values to the speed under control conditions, but they had a lower tolerance to frost, i.e., the size of the rosette under frost was more negatively affected. Hence, the most discriminating traits were not among those differing more consistently with elevational distribution of species, including leaf area and LDMC, but traits that differed between the two groups of species under a particular thermal environment. Furthermore, they depicted aspects of growth and not leaf function or leaf resistance. These results are novel, but possibly applicable to many other taxonomic groups. We do not know yet because there are hardly any comparative study in which species were raised under different temperature regimes and in which growth trajectories were analysed for their many facets, which our study motivates to do.

Past evolutionary processes and phylogenetic inertia

Evolutionary models, whether they depicted genetic drift, stabilizing selection or directional selection with two optima, differed in the number of times they were the best under the testing of all traits measured in the three growth environments. Models depicting genetic drift were rarely supported, for any trait in the three thermal growth environments. The model of stabilizing selection came in second, and the one considering divergent selection acting between low- and high-elevation species first. This result supports the importance of divergent selection in niche evolution (Schluter 2001). Furthermore, evidence for divergent adaptation between low- and high-elevation species was more common for mild conditions and the regular occurrence of heat compared to frost. Apparently, the signature of evolution of a trait depends on the environment in which it is expressed. This may also be the environment in which selection happened in the wild. This insight that there is a considerable variation in the evolutionary response of traits depending on the environment in which they are expressed is important for future macroevolutionary work. Comparative studies typically rely on measurements taken in the field or on collection material (e.g., Luxbacher and Knouft 2009; Edwards and Smith 2010) or after raising organisms under standard conditions (e.g., Kellermann et al. 2012; Mason and Donovan 2015) While the former brings the problem of the inability of separating the effect of genetics from the environment, the latter has the flaw that the adaptive potential of a trait may not be detected as the environment is not the one in which divergence is expressed.

Coupled with the pattern of more pronounced trait divergence under some environmental conditions, phylogenetic inertia of traits was found to be environment dependent. In our study, the mild and heat treatments were not only the more discriminating among high- and low-elevation species, they were also the more limiting regarding phylogenetic inertia. Phylogenetic half-life was 36% higher in these two environments compared to the regular occurrence of frost. Part of the reason may be that it was the mild and the warm growth environment that had more traits with divergent optima for low- and high-elevation species, which are more likely to reveal a pattern of phylogenetic

inertia. However, for a number of trait-environment combinations, high phylogenetic half-life was found for traits for which the best-supported evolutionary model was not two optima. This suggest that traits were constrained asymmetrically and that adaptation to cold seems easier. Similar findings were made for critical thermal limits, with results suggesting that heat tolerance is largely constant across species as opposed to cold (Araújo et al. 2013). These types of results motivated the general hypothesis that adaptation in response to thermal stress is more evolutionary constrained for the heat than cold (Herrando-Pérez 2013; Bozinovic et al. 2014). Our study adds that environmental conditions within the general niche space differentially affects the evolutionary trajectory, both in direction and its speed.

Phylogenetic conservatism was often significant but generally low, with a few traits being exceptional. These included seed size, asymptotic size, leaf number, leaf size under mild conditions, leaf dissection, heat resistance when raised under regular occurrence of heat, and heat tolerance in asymptotic size. Hence, apart from traits related to plant size, coping with heat showed evolutionary inertia, in line with the hypothesis of asymmetry in thermal evolution discussed above. The two most discriminating traits between low- and high-elevation species expressed under heat had lower but considerable half-lives, of 0.2 Mya for the time until the fastest growth was reached and 1 Mya for tolerance in the speed of growth. Traits more relevant regarding the cool aspects of the thermal niche, including resistance and tolerance to frost, had intermediate to low phylogenetic niche conservatism. cold resistance for the lower negative temperatures with separate optima for low- and high-elevation species had a half-life of 1 Mya, while the one for frost tolerance in asymptotic size was 20’000 years. Phylogenetic conservatism for traits coping with frost or cold may be variable, and the literature is supportive of this. Some have suggested that cold-induced traits are hard to evolve (Donoghue 2008; Sakai and Larcher 2012), and a number of studies described higher inertia in freezing resistance or cold tolerance (Kellermann et al. 2012; Hawkins et al. 2014; Pérez et al. 2014). However in

angiosperms, as an example, many cold adaptations were found, suggesting great evolutionary flexibility (Preston and Sandve 2013).

Trade-off, the role of the environment, and the consequence for disparate distribution

We identified an important trade-off between two distinct traits which contributed most to differentiating high- and low-land species: fast growth under heat and frost tolerance. Our results are in agreement with other studies, showing a negative association between growth and cold or frost resistance (Loehle 1998; Koehler et al. 2012; Molina-Montenegro et al. 2012; Bucher et al. 2019). A first potential cause of the trade-off may be correlational selection, which we discuss in more depth below. Such a mechanism has for example been suggested across a predation gradient in amphibians, where species are either active, exposed to predators but fast growers, *vs.* species that are inactive, overseen by predators, but slow growers (Urban 2007). A second potential cause of the trade-off may be genetic, caused by physical linkage or antagonistic pleiotropy (Roff and Fairbairn 2012). Here transplant experiments in nature and microevolutionary studies on the presence of within species trade-offs are needed to tease apart the trade-off of living at low- *vs.* high elevation.

Selection on high-elevation species may act via the short growing season at high elevation. During the short vegetative period, the average temperature can be relatively low, and two options seem to be likely, apart from higher frost resistance: adaptation to grow well under cooler conditions – a shift in the thermal optimum for growth, or to fasten development under good conditions – to increase the peak of the growth curve. Several trait differences in high-elevation species point in the direction of the latter scenario. Under the regular occurrence of heat, speed of growth was fastened. Adaptive models pointed in the direction of lower dry matter and higher leaf area (SLA) under warmer conditions, associated with higher assimilatory capacity, even though final size was not higher. In line higher photosynthetic rate was recorded in highland herbaceous species under lowland

temperature (Mächler and Nösberger 1977) or during daily warm spells (Körner and Diemer 1987). Being fast is likely important for high-elevation species as the inability to successfully finish reproduction within a season has been proposed a limiting factor for latitudinal range limits (Morin et al. 2007). Similar results for upper range limits were obtained in a recent niche-modelling study on alpine Brassicaceae (Patsiou et al. 2020). For low-elevation species, rapid development may be too costly, as it may for example involve smaller plant size.

Lowland plants were found to be more frost tolerant; their loss in plant size was lower under frost exposure compared to high-elevation species. Although counterintuitive, past research found evidence for an increased risk of freezing damage in lowland plants (Lenz et al. 2013). Furthermore, the extent of freezing resistance was related to winter snow protection (Briceño et al. 2014), with plants commonly protected with a snow layer from early fall to late spring being less frost resistant that those living in an environment with little snow. Several low-elevation Brassicaceae are winter-green, i.e., they germinate in late autumn and the rosette grows during the wintertime. Some species even reproduce during this season and die before the end of spring, which requires frost tolerance. In contrast, high-elevation species consistently experience a snow layer during winter and their lack of frost tolerance may be due to costs. On the flip side, their low-elevation limit may be due to an inconsistent snow layer in winter.

CONCLUSION

Our study highlights that the most discriminating traits separating high- from low-elevation Brassicaceae species are their ability to speed up growth under warm to hot conditions, and their lower frost resistance. High-elevation plants cannot maintain vegetative size when frosts occur. Results suggest a general trade-off between exploiting the short vegetation period at high elevation and being less good with frost. The trade-off could be a result of correlational selection differing

among high- and low-elevation sites, and/or genetic trade-offs. Most notably, these traits were not the only ones to differ between high- and low elevation species, and they were also not those that were consistently expressed across the experimental growth environments under which we raised the plants. Furthermore, none of these most discriminating traits between low- and high-elevation species involved leaf function or resistance traits, but traits related to growth. Furthermore, we found evidence that while divergent adaptation to heat was more common than to frost, adaptation to heat was more constrained.

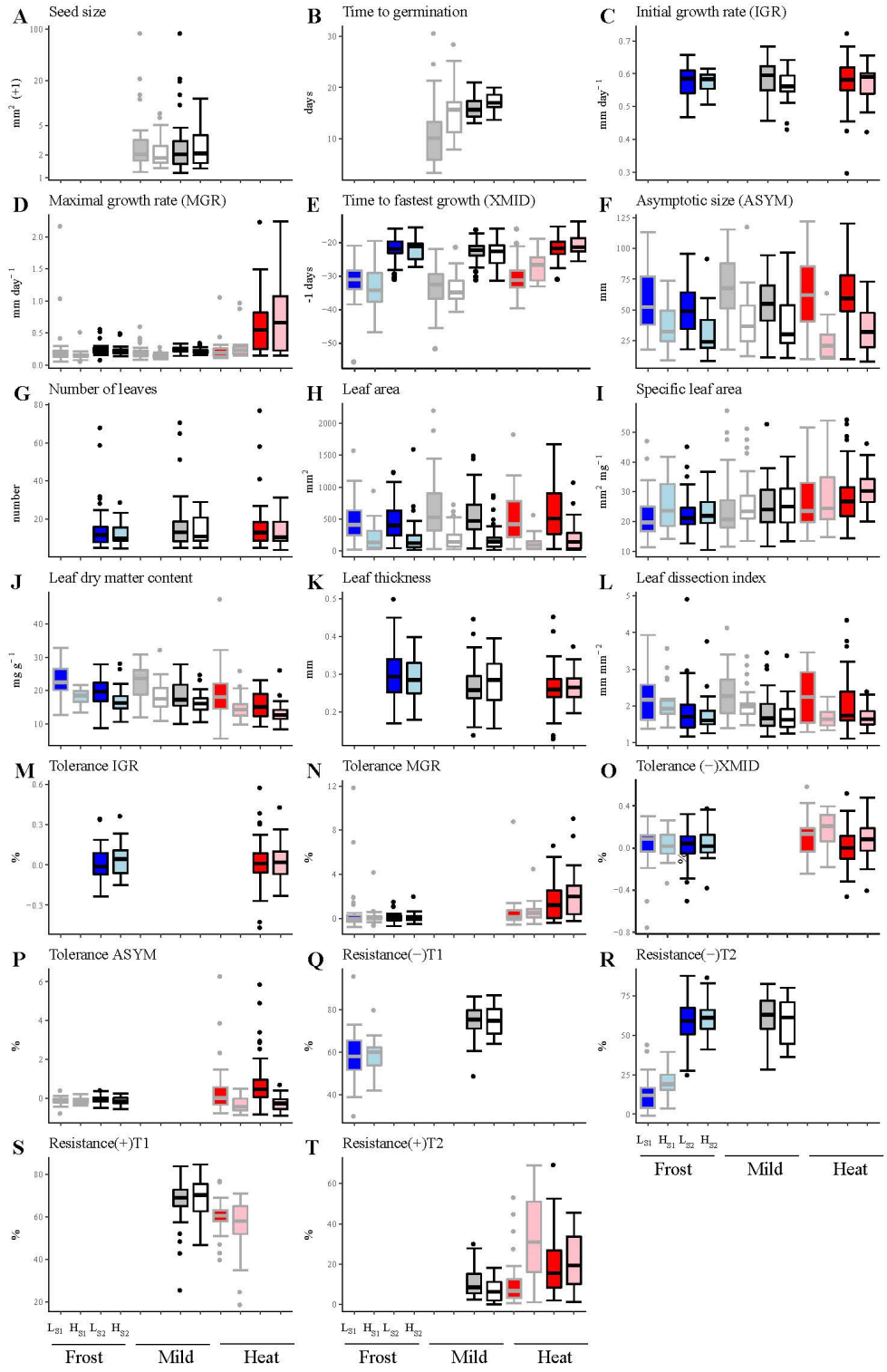
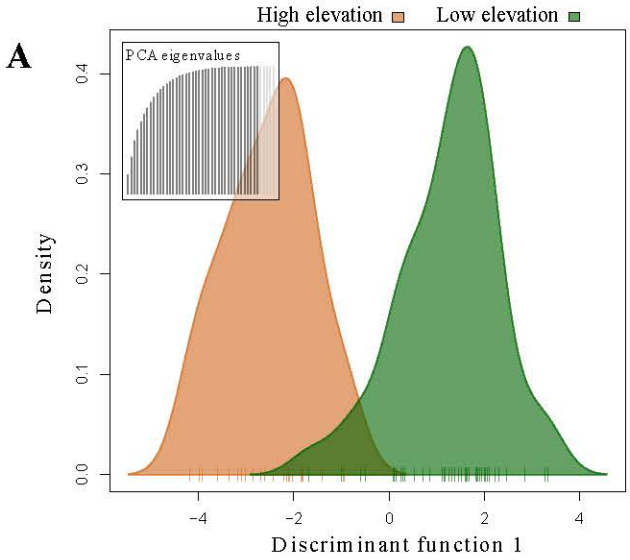
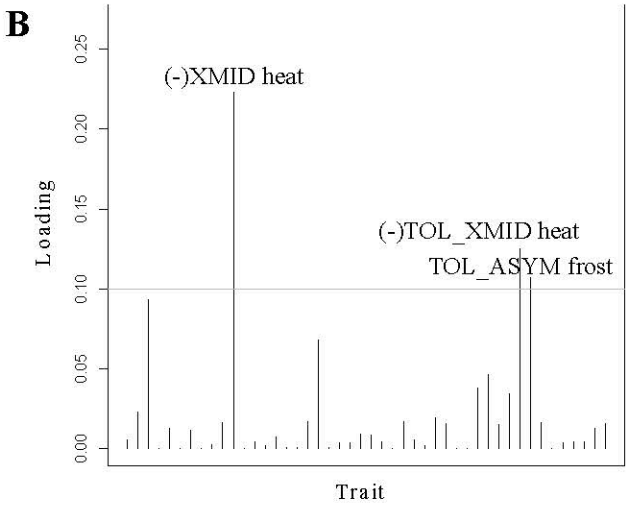


Figure 1 Boxplot showing the distribution of species-mean trait values. Colours inside boxes represent the treatments (blue for frost, greyscale for control and red for heat), while the intensity represents elevation in which species occur (darker colours for low elevation and lighter colour for high elevation). Contour colour is used to distinguish between the sowings (clear contour is used for sowing S1 and black contour for sowing S2). Electrolyte leakages (RES) were grouped together and referred as T1 (47/-6 °C S1, 45/-5 °C S2) and T2 (52/-12 °C in S1 and 50/-10 °C S2). XMID and was multiplied by -1 in order to have highest values representing faster growth (referred as (-)XMID).





C

	(-)XMID heat	(-)TOL_XMID heat
TOL_ASYM frost	0.17	**-0.29 ***
(-)XMID heat	1	**0.30 ***

Figure 2 Results of discriminant analysis of principal components and multi-trait correlation. A. Density distribution of the discriminant function partitioned between the two elevational classes (*left* High-, *right* Low- elevation). Top left the correspondent number of PCA eigenvalues retained after alpha-selection; B. Loadings plot on the full dataset showing the most relevant traits in characterizing elevational groups; C. Pearson's correlation (*r)* between traits with highest load. XMID was multiplied by -1 in order to have highest values representing faster growth (referred as (-)XMID).

Table 1 Summary of models testing for the effect of treatment during plant growth (regular frost [F], mild conditions [M], and regular heat [H]), median elevation of species distribution and their interaction on plant traits

	Trait	Trait ID	Posterior means									
			Treatment (F | M | H)				**Elevation**		**Treatment (F | M | H) × elevation**			
			F *vs* M		H *vs* M				Slope of elevation under F *vs*. M		Slope of elevation under H *vs*. M	
	Seed size	SSIZ					-0.026					
	Time to germinate	TGER					0.302					
Growth	Initial growth rate	IGR	-0.004		-0.008		-0.005		0.007		0.007	
Growth	Maximal growth rate	**MGR**	0.007		**0.246**	***	-0.026		0.021		**0.084**	**
Growth	Time to fastest growth	**(-)XMID**	**0.934**	*	**3.112**	***	-0.602		0.186		**1.723**	***
Growth	Asymptotic size	**ASYM**	**-0.063**	***	**-0.068**	**	-0.017		-0.012		**-0.06**	***
Growth	Number of leaves	NLEA	**-0.027**	*	0.001		-0.005		-0.004		-0.010	
Leaf traits	Leaf area	**LA**	**-0.072**	**	**-0.113**	***	**-0.155**	***	0.014		**-0.050**	*
Leaf traits	Specific leaf area	**SLA**	**-3.191**	***	**3.131**	***	-0.081		-0.042		1.255	(*)
Leaf traits	Leaf dry matter content	**LDMC**	0.545		**-3.094**	***	**-1.427**	**	0.163		0.047	
Leaf traits	Leaf thickness	LTh	**0.021**	**	-0.006		0.007		-0.006		-0.003	
Leaf traits	Leaf dissection index	**LDI**	-0.004		-0.007		0.018	(*)	0.008		**-0.020**	**
Thermal tolerance *s.l.*	Frost resistance (-5/-6°C)	RES(-)T1					-0.558					
Thermal tolerance *s.l.*	Frost resistance (-10/-12°C)	**RES(-)T2**	**(S1)**				**4.542**	**				
			(S2)	-2.472			0.448		1.235			
Thermal tolerance *s.l.*	Heat resistance (+45/47°C)	RES(+)T1					0.749					
Thermal tolerance *s.l.*	Heat resistance (+50/52°C)	**RES(+)T2**	**(S1)**				**9.009**	**				
			(S2)		**0.249**	***	**-0.101**	**			0.075	(*)
					H *vs* F		**Elevation**				**Slope of elevation under H *vs* F**	
Thermal tolerance *s.l.*	Tolerance IGR	TOL_IGR			0.003		0.014				0.011	
Thermal tolerance *s.l.*	Tolerance MGR	**TOL_MGR**			**0.822**	***	0.086				**0.124**	*
Thermal tolerance *s.l.*	Tolerance XMID	**(-)TOL_XMID**			-0.018		-0.010				**0.050**	**
Thermal tolerance *s.l.*	Tolerance ASYM	**TOL_ASYM**			**0.072**	**	0.007				**-0.136**	***

Full details are provided in Supplementary material A2. Posterior means are given, relative to the baseline of average elevation and mild growth conditions. For tolerance traits, the coefficients express differences between estimates under heat compared to those under frost. Bold highlight trait with significant effect of elevation or its interaction. P-values (pMCMC) are indicated (with significant coefficients in bold): (*) > 0.1, * > 0.05, ** > 0.01, *** > 0.001.

Table 2 Summary of best evolutionary models for traits assessed in the three growth environments (regular frost, mild and regular heat) and the suggested trait optima (θ) when the best model was OUM

		Treatment								
		Frost			Mild			Heat		
	Trait ID	Best model	θ_{LOW}	θ_{HIGH}	Best model	θ_{LOW}	θ_{HIGH}	Best model	θ_{LOW}	θ_{HIGH}
	SSIZ	.			BMM/OU1			.		
	TGER	.			OUM	13.51 ± 2.42	16.46 ± 0.97	.		
Growth	IGR	OU1			OUM	0.58 ± 0.00	0.56 ± 0.00	OU1		
	MGR	BMM/OU1			OUM	0.20 ± 0.04	0.18 ± 0.04	OU1		
	(-)XMID	OU1			OU1			OUM	-26.08 ± 4.14	-23.92 ± 3.19
	ASYM	OUM	55.79 ± 3.89	34.36 ± 2.44	OUM/OU1	62.31 ± 7.19	40.60 ± 1.67	OUM	67.04 ± 1.72	18.47 ± 10.60
	NLEA	OU1			OU1			OU1		
Leaf traits	LA	OUM	466.15 ± 10.62	221.73 ± 8.73	BMM			BMM/OUM	619.10 ± 0.00	177.43 ± 0.00
	SLA	OU1			OU1			OU1/OUM	27.68 ± 0.00	31.56 ± 0.00
	LDMC	OUM	21.55 ± 1.69	17.30 ± 0.72	OUM	20.43 ± 1.80	17.13 ± 1.24	OU1/OUM	16.20 ± 0.00	12.63 ± 0.00
	LTh	OU1			OUM	0.26 ± 0.00	0.30 ± 0.00	OU1		
	LDI	OU1			OUM/OU1	2.05 ± 0.23	1.87 ± 0.16	OUM	2.17 ± 0.12	1.55 ± 0.02
Thermal tolerance *s.l.*	RES(-)T1	OU1			OU1			.		
	RES(-)T2	OUM/OU1	35.03 ± 22.25	40.02 ± 20.25	OU1			.		
	RES(+)T1	.			OU1			OUM	59.75 ± 0.20	47.74 ± 2.84
	RES(+)T2	.			OUM	11.22 ± 0.00	6.69 ± 0.00	OUM/OU1	14.96 ± 3.45	27.03 ± 3.80
	TOL_IGR	OU1			.			OU1		
	TOL_MGR	OU1			.			OU1/OUM	1.52 ± 0.00	2.44 ± 0.00
	(-)TOL_XMID	OU1			.			OU1/OUM	0.00 ± 0.00	0.11 ± 0.00
	TOL_ASYM	OU1/OUM	-0.05 ± 0.00	-0.14 ± 0.00	.			BMM/OUM	0.78 ± 0.00	-0.31 ± 0.00

The table presents the best fitting model (mean AICc value) obtained for each trait-treatment combination based on the consensus of 100 simulations (detailed information in Supplementary materials A3, A4, A5). In case analyses on S1 and S2 showed differences in best-fitting model, both of them were included (S1 on the left, S2 on the right). BM: Brownian-Motion; BMM: Brownian-Motion with different speed for the different regime; OU1: Ornstein-Uhlenbeck with single optima, OUM: Ornstein-Uhlenbeck with different optima for the different regimes. '-' is used when a trait was not assessed for the treatment.

Table 3 Trait evolutionary half-life (± standard deviation)

		Treatment														
		Frost					Mild					Heat				
	Trait ID															
	SSIZ	.		.			8.412	±	0.065	*		.		.		
	TGER	.		.			1.081	±	0.305	*		.		.		
Growth	IGR	0.024	±	0.011	*	S2	0.090	±	0.065	ns	S2	0.030	±	0.008	*	S2
	MGR	2.355	±	0.127	*		0.090	±	0.043	*		0.733	±	0.017	*	
	(-)XMID	0.158	±	0.092	*		0.346	±	0.022	*		0.196	±	0.103	*	
	ASYM	3.419	±	0.176	*		6.013	±	0.431	*		10.630	±	2.650	*	
	NLEA	3.709	±	0.054	*	S2	7.148	±	0.108	*	S2	5.992	±	0.063	*	S2
Leaf traits	LA	2.228	±	0.130	*		6.816	±	0.581	*		11.264	±	2.039	*	
	SLA	2.747	±	0.121	*		1.725	±	0.013	*		0.403	±	0.028	*	
	LDMC	1.732	±	0.816	*		0.796	±	0.117	*		1.188	±	0.284	*	
	LTh	0.101	±	0.032	*	S2	2.502	±	0.160	*	S2	0.105	±	0.139	ns	S2
	LDI	5.150	±	0.090	*		4.347	±	0.274	*		7.099	±	0.772	*	
Thermal tolerance *s.l.*	RES(-)T1	1.924	±	0.077	*	S1	1.600	±	0.079	*	S2	.		.		
	RES(-)T2	1.091	±	0.392	*		0.487	±	0.102	*	S2	.		.		
	RES(+)T1	.		.			0.213	±	0.243	*	S2	5.008	±	1.186	*	S1
	RES(+)T2	.		.			0.202	±	0.243	ns	S2	0.224	±	0.127	*	
	TOL_IGR	0.252	±	0.049	*	S2	.		.			0.028	±	0.011	*	S2
	TOL_MGR	1.686	±	0.051	*		.		.			0.519	±	0.030	*	
	(-)TOL_XMID	0.386	±	0.026	*		.		.			0.955	±	0.129	*	
	TOL_ASYM	0.020	±	0.005	*		.		.			4.526	±	0.338	*	

Mean values ± standard deviation (SD) of phylogenetic half-life (estimated from OU1 + OUM) for traits within treatments and across sowing (S1+S2, 'Global' in Supplementary material A5). '.' : if trait not available (e.g., not measured in the treatment or if best model is "BM" type); values of phylogenetic half-life are based on ARD + ER reconstruction model (for each model, 100 independent stochastic character maps with 'High' and 'Low' regime) and ‘S1/S2’ if trait was measured in only a specific round of sowing. Full details can be found in Supplementary material A3 and A5. Values are in Mya. Significance in half-life (*) was calculated by mean - 1.64 × SD > 0.

Table 4 Summary of the results for each trait/treatment

	Trait ID	Effect of elevation							Phylogenetic inertia			Trade-offs					
		MCMCglmm				OUM			Half-life			DAPC			*r*		
		Elev	F	M	H	F	M	H	F	M	H	F	M	H	F	M	H
	SSIZ		.		.	.		.		✓		.		.	.		.
	TGER		.		.	.	✓	.				.		.	.		.
Growth	IGR						✓										
Growth	MGR			c	✓(+)		✓										
Growth	(-)XMID			c	✓(+)			✓						✓			
Growth	ASYM			c	✓(-)	✓	✓	✓	ns/✓	✓	✓/ns						
Growth	NLEA									✓	✓						
Leaf traits	LA	✓(-)		c	✓(-)	✓		✓			✓/ns						
Leaf traits	SLA			c	✓(+)			✓									
Leaf traits	LDMC	✓(-)		c		✓	✓	✓									
Leaf traits	LTh						✓										
Leaf traits	LDI	✓(+)	□	c	✓(-)		✓	✓	□ ns/✓	✓/ns	✓						
Thermal tolerance *s.l.*	RES(-)T1				.			.						.			.
Thermal tolerance *s.l.*	RES(-)T2	✓(ns/+)			.	✓		.						.			.
Thermal tolerance *s.l.*	RES(+)T1		.			.					✓/ns	.			.		
Thermal tolerance *s.l.*	RES(+)T2	✓(-/+)	.	c	✓(+)	.	✓	✓				.			.		
Thermal tolerance *s.l.*	TOL_IGR			.			.						.			.	
Thermal tolerance *s.l.*	TOL_MGR		c	.	✓(+)		.	✓					.			.	
Thermal tolerance *s.l.*	(-)TOL_XMID		c	.	✓(+)		.	✓					.	✓		.	✓
Thermal tolerance *s.l.*	TOL_ASYM		c	.	✓(-)	✓	.	✓	□ □	□	✓/ns	✓	.		✓	.	

✓ reflects a significant role species elevational distribution: in *MCMCglmm* also when the interaction with treatment was significant ('c' indicates what the comparison was with, the sign between parentheses the direction of effect [with differences between sowing S1 and S2 further by '/']), in evolutionary modelling when OUM was the best model, in the analysis of half-life when that one >3Mya, in trade-offs under *DAPC* and a threshold of th = 1, and in the analysis of trait correlations. "." indicates that a trait was not assessed.

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CHAPTER 2

Niche breadth and range size in heterogeneous environments: a comparative study in Middle-European Brassicaceae species

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Acknowledgements

We thank Georg Armbruster, Olivier Bachmann, Kay Lucek, Michela Meier, Jens Paulsen, Antoine Perrier, Susanna Riedl, and Darío Sánchez-Castro for help with data collection and for fruitful discussions. We thank Theofania-Sotiria Patsiou for sharing species occurrence data and all the field botanists who contributed to the collection of occurrence data for the InfoFlora database.

ABSTRACT

Species are geographically restricted. Although in the past years the study of range limits has seen renewed interest, less attention has been devoted to range size. Theoretical work suggests that larger ranges are associated with more variable conditions, which require wider niche breadth and selection for plastic (generalist) genotypes. We used macroevolutionary comparisons involving 90 Brassicaceae species differing in elevational range size to test for a positive association between range size, performance breadth or trait elasticity on the one hand, and spatial and temporal thermal variability on the other hand. Plants were grown under three temperature treatments (regular frost, mild, regular heat), and thermal performance breadth, thermal optima, and trait elasticity across pairs of environments were calculated. Data were related with environmental descriptors of spatial and temporalthermal variability where each species occurs in nature. Our results indicated that spatial thermal variability was associated with the range size but that it was unable to predict variation in trait elasticity or performance breadth. Furthermore, a negative association between temporal thermal variability and trait elasticity was observed. However, trait elasticity was not associated with performance breadth but decreased with increasing thermal specialization. Overall, little evidences for adaptive constraints were detected, except that plasticity in frost and heat resistance showed a trade-off and that phylogenetic niche conservatism for temporal thermal variation was detected. Results suggest that an interplay between adaptation to thermal heterogeneous environments and thermal specialization can explain elevational range sizes.

Key words: Climate variability hypothesis - Rapoport's rule – Generalist-specialist trade-off – Niche breadth – Phylogenetic signal – Plants – Thermal plasticity – Stress-tolerance strategy

INTRODUCTION

Species vary in range size, but the factors causing this phenomenon remain not completely understood. The fundamental question of causes of range limits has fascinated ecologists and evolutionary biologists alike in the last two centuries (i.e., *species' range limits*, e.g., von Humboldt and Bonpland 1805). In contrast, less attention has been devoted to variation in the size of colonised areas of species (i.e., *species' range size,* e.g, Gaston 2003) despite its direct impact on biodiversity and conservation. A number of hypotheses have been proposed, from sampling artefacts to phylogenetic non-independence and variation in niche breadth (summarized in Gaston 2003). During the last decade, one of them has attracted increasing support: the niche-breadth hypothesis (Slatyer et al. 2013). In short, the hypothesis posits that highly tolerant species are expected to have larger geographic ranges (Brown 1984; hypotheses described here and below are summarized in Fig. 1). Therefore, the hypothesis attributes a key role to physiology, but its role is still under debate, and aspects of thermal distribution have been largely neglected.

The niche-breadth hypothesis (Brown 1984) builds on the niche concept. The niche is defined as the abiotic and biotic conditions needed for a species to maintain viable populations (Hutchinson 1957). The niche breadth of a species is the width of the performance curve along gradients of conditions. Support for the niche-breadth hypothesis is given if niche breadth and geographical range size are positively related. The reasoning is that tolerance to a wider range of environmental conditions means that more habitats are suitable for a species. There are many studies supporting the niche breadth-range size association (e.g., Gaston and Blackburn 2008; Trakimas et al. 2016). In a recent meta-analysis including 63 studies, Slatyer et al. (2013) identified positive relationships between several types of variables depicting tolerance, diet and habitat, and range size, but studies on physiological tolerance were less than 10%, even though most species' ranges can be explained by climate alone (Lee-Yaw et al. 2016).

Focusing on the climatic dimension of the niche, Rapoport's rule predicts increased range size in species occurring at higher compared to lower latitudes (Rapoport 1982). The rule is based on the hypothesis that the climate is more variable at higher latitudes, and climatic variability selects for broader climatic tolerance (*climatic-variability hypothesis;* Stevens 1989). Rapoport's rule has been predicted to be valid also across elevational gradients (i.e., elevational Rapoport's rule, Stevens 1992). Since elevation gradients exhibit strong abiotic variation over short geographical distances (-0.5K for each 100m-increase in elevation) and are characterized by more increasing temporal climatic variability (Brinck 1974), selection should favour broader climatic tolerance in species occurring at higher elevations. Consequently, they should have larger range sizes. In more general terms, species inhabiting regions that are climatically heterogeneous, both at the temporal or spatial scale, should evolve larger climatic tolerance than those from climatically stable ones, and have larger range sizes. In contrast, species living in environmentally more homogeneous regions should have narrower tolerance, increased climatic optima (e.g., Sunday et al. 2011) and possibly smaller ranges.

Climate and climate variability, and here especially temperature, affect biochemical reactions, species performance and population growth, and may impose selection (Kingsolver 2009). This may be especially true for ectotherms whose activity is strongly determined by environmental temperature, and sessile organism that cannot change their position by avoiding thermal extremes. Surprisingly, even if temperature is supposed to be one of the prevailing limiting factors to species, only few studies have tested explicitly for the role of temperature heterogeneity on thermal tolerance. In fact, while a number of studies attempted to link latitude and thermal sensitivity (e.g., van Berkum 1988; Addo-Bediako et al. 2000; Stillman and Somero 2000; Sunday et al. 2011; Wos and Willi 2015), only a few have directly tested for a positive relationship between climate, occurrence and range size (e.g., Pither 2003; Yu et al. 2017; Diamond and Chick 2018) or included in their study physiological tolerance (Calosi et al. 2008, 2010; Luna et al. 2012; Sheth and Angert 2014) or trait plasticity (De Araujo et al. 2019).

Plasticity has long been suggested to be associated to broader range size, especially in sessile organism (Bradshaw 1965). This is especially due to the ability of plastic genotypes to render different trait values under different environmental conditions, thus maintaining higher-fitness across multiple environments (Klopfer and MacArthur 1960; Bradshaw 1965; Sultan 1987; Pigliucci 2001). Plastic response to environmental conditions has been documented for many important ecologically traits (Sultan 2000) and has been frequently reported as adaptive (e.g. Poorter and Lambers 1986; Valladares and Pearcy 1998; Dudley 2004). In particular, heterogeneous environments are expected to promote the evolution of plasticity (Bradshaw 1965; Via and Lande 1985; Gabriel and Lynch 1992; Gomulkiewicz and Kirkpatrick 1992; Gabriel et al. 2005), and species under both temporally or spatially varying environments should be selected for increased plasticity (Gabriel et al. 2005; Gunderson and Stillman 2015). This led to the expectation that there is a positive link between phenotypic plasticity and geographic range size, but evidences have been contradictory. On the one hand, empirical studies corroborated a positive relationship between plasticity to climate and wider niches (Molina-Montenegro and Naya 2012; Bonino et al. 2015; Lovell and McKay 2015; Lacher and Schwartz 2016; Rutherford et al. 2017; Zeng et al. 2017; Aspinwall et al. 2019) and a reduction in plasticity in species with increased thermal specialization (e.g., Kelly et al. 2013; Heerwaarden et al. 2016; Gilbert and Miles 2019). On the other hand, studies failed to associate plasticity with distribution or commonness (González and Gianoli 2004; Pohlman et al. 2005; Overgaard et al. 2011; Dostal et al. 2017; Hirst et al. 2017; Mitchell et al. 2017; De Araujo et al. 2019; Fortunel et al. 2019), or.

Studies on temperature and elevational gradients have been particularly scarce, even though the latter have the benefit of a restricted spatial scale and therefore being affected by fewer confounding effects. Furthermore, elevational gradients are positively associated with an increase in temperature variability over time and space. At high elevation, seasonal and daily temperature variation can be as high as 5 K (with peak of 15 K) as reported in Körner (2003). Furthermore,

microclimatic spatial pockets may differ in temperature; e.g., Inouye (2008) reported variation of 2 °C over 12 meters, or variation in 56 K between the most extreme temperatures during the growing season were reported in *Ranunculus glacialis*, with daily thermal-variation in mid-summer of more than 20 K (Körner 2003). During the last twenty years, a number of studies have addressed the role of elevation on plasticity, focusing on phenology and particularly, on flowering (Gugger et al. 2015; Dai et al. 2017; Schmid et al. 2017; Trunschke and Stöcklin 2017), on growth and defence (Bakhtiari et al. 2019), drought and climate change (Hamann et al. 2018), and local adaptation (Villemereuil et al. 2018). However, the association between thermal plasticity and elevational range size is still largely unknown.

To elucidate the relationship between plasticity and range size (Fig. 1), two important points must be considered. First, it is crucial to make a clear distinction between eco-physiological traits and fitness or traits strongly affecting fitness under any condition (Violle et al. 2007). In fact, whether great variation in the former can allow the modulation of the physiological response in a heterogeneous environment, a great variability in the latter will be a sign of maladaptation since fitness will not be maintained across the varying environments. Secondly, focusing on single species can produce misleading generalizations as the level of variation in phenotypes across environments can vary among species (Bradshaw 1965; Pemac and Tucić 1998; Valladares et al. 2002b,a, 2005). Furthermore, phylogenetic relatedness may affect niche breadth and ecological similarity of species may exist due to niche conservatism (Barnagaud et al. 2014; Kerkhoff et al. 2014; García-Navas and Westerman 2018). One way to overcome these problems is the macroevolutionary approach, of studying many species and accounting for shared history.

Here we studied the extent to which range size, niche breadth and plasticity in functional traits are associated with spatial and temporal thermal variation, and whether trade-offs in plasticity to frost and heat exist. Analyses were performed in a macroevolutionary framework. The study involved 90 Brassicaceae species from the European Alps, having an elevational range width from 12 to 1300 m.

Plants were raised under three temperature treatments: control conditions, and the regular occurrence of either frost or heat. Performance estimates were used to quantify the thermal niche breadth, and values of nine eco-physiological traits were used to calculate a thermal plasticity index (RDPI, Valladares et al. (2006)). RDPI was calculated at a species level. We used the term "elasticity" (and not plasticity) to reflect the ability of a trait to change in response to different environments. The following questions were addressed: i) Are elevational range size, breadth of performance or trait elasticity positively related with increased spatial and temporal variation in the thermal regime? ii) Is trait elasticity positively related with thermal performance breadth? Is there a trade-off between coping with frost and heat, or between thermal specialization and plasticity? And iii) how phylogenetically constrained are range size, thermal niche breadth and trait elasticity?

MATERIAL AND METHODS

For this study, the same species and traits measured in Maccagni and Willi (2020) were used. Only traits measured in the round of sowing with a gibberellic acid treatment ('S2') were considered, and that were assessed under more than one specific environment. The choice of species, the thermal treatments applied during plant growth, and the traits assessed are summarized below (for a detailed description see Maccagni and Willi 2020).

Species choice and sampling

One hundred taxa belonging to the Brassicaceae family and naturally occurring from the colline to the alpine life zone in the Swiss Alps were selected. An exhaustive list of the species is available in supplementary material A1. Seeds of a species were collected from March to September during the years 2015-2017 at two different sites in the Swiss Alps, located at least 50 km apart from each other and preferentially in different biogeographic regions. The sites were at the most common elevation

for each species. For endangered species inscribed in the Red List 2002 (Moser et al. 2002), authorization for sampling was obtained by the respective Cantonal authority.

Sowing, growing conditions and treatments

Design – The experimental design involved the raising of 100 taxa, each represented by 2 populations and 3 seed families per population, i.e. 6 seed families per species. Plants of each family was raised under 3 temperature treatments, and used as biological replicates at the species level. The experiment was split into 6 blocks, with a different seed family per species, and each block contained the 3 temperature treatments (regular frost, mild, regular heat). The final design resulted in 1'800 individuals (100 taxa × 6 families each in a different block × 3 treatments = 1'800 individuals). Seeds of each seed-family were haphazardly selected.

Seeds were incubated in 500 µl of gibberellic acid solution (500 ppm, Merck KGeA, Dornstadt, Germany) for 1 week in dark and cold (4 °C constant; Climecab 1400 Kälte 3000 AG, Landquart, Switzerland). After this period, seeds were sown in multipot-trays (0.06 L, 54 pots per tray Ø 4.4 cm, BK Qualipot; gvz-rossat.ch, Otelfingen, Switzerland) and transferred to growth chambers (MobyLux GroBanks, CLF Plant Climatics, plantclimatics.de, Wertingen, Deutschland). All growth chambers were located inside a PlantMaster (CLF, Plant Climatics, plantclimatics.de, Wertingen, Deutschland) with controlled temperature and humidity. Trays were kept at 15/18 °C night:day, 75% relative humidity (RH), light:dark 8:16 h at 150 µmol m^2 s^{-1} (fluorescent white lamps and red-LED). After 3 weeks, excess seedlings were used to fill pots without any germination. In week 4, germinated plants were moved in Climecabs and were subjected to three temperature treatments.

Treatment – Plants were subjected to three temperature treatment: "frost" (F), "mild/control" (M) and "heat" (H). Frost: 20 °C (day), then -2 °C for 1 h (-4.8 K h^{-1}; night), back to 20 °C (+7.3 K h^{-1}; night), 20 °C (day). Mild: 20 °C constant. Heat: 20 °C (day), then 40 °C for 1 h (+5.5 K h^{-1}; day),

back to 20°C (-8.3 K h^{-1}; day), 20 °C (night). All treatments were conducted at a daily cycle of 12:12 h light:dark, 300 µmol m^2 s^{-1} of light (LED white lamp) and 75% relative humidity. Plants were kept under these conditions until the 9th week after sowing.

Trait assessment, performance, and elasticity

Growth (IGR, MGR, XMID, ASYM, NLEA) – The length of the 2 longest leaves of each plant was measured weekly (in mm), and data was used to model the growth trajectory based on a three-parameter logistic model. The asymptotic size (ASYM), the maximal growth rate (MGR, i.e., 1 $scale^{-1}$) and the time to fastest growth (XMID) were obtained using the 'SSlogis' function. Initial growth rate (IGR) was derived from the knee of the exponential phase of the curve with the 'maxcurve' {soilphysics} (da Silva and de Lima. 2017) and 'deriv' functions. As an additional estimate of growth, the number of leaves on day 35 of treatment was retained (NLEA).

Leave functional traits (LA, LDI, SLA, LDMC, LTh) – During week 8 of treatment, 2 fully elongated leaves from the 3rd whorl were harvested from each plant and used for leaf-trait assessment. Leaves were scanned (CanonScan, LiDe120, Canon, Tokyo, Japan) and analysed by ImageJ to obtain leaf area (in mm^2, LA) and perimeter (in mm). The leaf dissection index (LDI) was calculated as the ratio between perimeter and area following Fourier's transformation (Kincaid and Schneider 1983). Specific leaf area (SLA) was calculated as area over dry weight (mm^2 mg^{-1}) and leaf dry matter content (LDMC) as the percentage of dry weight over fresh weight (mg g^{-1}). Leaf thickness (LTh) was estimated on fresh leaves using a mini-digital thickness gauge (0.01 mm, digitalmicrometers.co.uk).

Frost and heat resistance (electrolyte leakage, RES) – During week 9 of treatment, leaves from the 3rd to 5th whorl were selected. From healthy and fully developed leaves a circular leaf disc of 6mm diameter was punched out and put in a separate 15 ml falcon tube (Sarstedt, PP, 120x17 mm, Nümbrecht, Germany). Each tube was subjected to a specific thermal treatment for 1h: -10 °C for

frost resistance (for plants in mild and frost conditions) and +50 °C to assess heat resistance (for plants in mild and heat conditions). After heat and frost treatment, 3 ml of dH_2O was added to each tube, and samples were kept in the dark at room temperature overnight to allow electrolytes to dissolve in the water. Electrolytes leakage was measured with a calibrated conductivity meter (Fe30/EL30, Mettler Toledo, Columbus, USA) before and after a boiling bath. The ratio between conductivity measured after treatment and conductivity after the boiling bath reflected the percentage of damage. Resistance values were obtained by 1 – damage, in percent; higher values indicate higher resistance.

Calculation of trait elasticity (RDPI) – Trait elasticity was calculated for each trait (except NLEA and ASYM as they were considered to represent performance) using the simplified relative distance plasticity index (RDPI, model 16 in Valladares et al. (2006)). For each trait-species-treatment combination, we calculated the mean trait value. Then, we calculated the elasticity as the absolute difference between the trait values of the different thermal environments (FH: Frost-Heat, MF: Frost-Mild, MH: Heat-Mild). Values were then divided by the sum of the values within the paired treatments, resulting in an elasticity index ranging from 0 (no-elasticity) to 1 (maximal-elasticity).

$$RDPIs = \frac{|\overline{Trait}_{env1} - \overline{Trait}_{env2}|}{\overline{Trait}_{env1} + \overline{Trait}_{env2}}$$

Thermal performance breadth and optima – For each species, performance was defined as the product of NLEA and ASYM and it was calculated for each treatment (i.e., Frost, Mild and Heat), and each treatment was assigned a new attribute (i.e., Frost = -1, Mild = 0 and Heat = 1). Then, for each species, three models were fit: quadratic (performance ~ I + treatment + treatment^2), linear (performance ~ I + treatment) and a null model (performance ~ I). The quadratic model was the best supported (by AIC, 'aictab' {AICcmodavg} (Mazerolle and et al. 2016) for the majority of the species. The equation was used to estimate the highest performance point (Y_{opt}) and the corresponding

temperature (X_{opt}). Classic approaches define niche breadth as the absolute distance between the two points of the curve reflecting 80%Y_{opt}, however 80%Y_{opt} fell outside the defined range [-1, +1] in some of our species. As consequence, to avoid value interpolation, we described thermal niche breadth as the mean of performance across treatments, divided by its standard deviation (the inverse of the coefficient of variation). Higher values reflect wider niche breadth (i.e. similar values of performance across environments), while lower values indicate more specialization.

Descriptors of elevational range size

Elevational range size was described as variation in elevation of occurrence of a species. For each species, we used data of previously published work (Patsiou et al. 2020), where raw occurrence data coming from an online national database (InfoFlora, infoflora.ch) where cleaned and thinned. In order to estimate the elevational range size, the elevation of each occurrence point of a species was extrapolated from a national digital elevation model with a resolution of 100 m (DEM100) with 'extract' {raster} (Hijmans and Van Etten 2016). The interquartile range of all elevation data for a species was calculated with the basic 'IQR' function (IQR_Elev). From the same dataset, the median elevation of occurrence was recorded.

Climatic variability was captured by two measures: the spatial temperature variability (Spatial_Var) and the temporal temperature variability (Temporal_Var). As with IQR_Elev. For each occurrence point, the average, maximum and minimum monthly temperatures were extracted from a climatic database for Switzerland. Monthly records were first merged with 'stack' {utils} and then temperature values were extracted for a time of the year with vegetative growth, the two months preceding peak flowering (month in range centre of reported flowering for Switzerland (Lauber et al. 1998), 'Fl') and for the two months after the end of winter, defined as average monthly temperature > 5°C, 'Wi'. Spatial_Var was calculated as the interquartile-range of monthly mean temperature, while Temporal_Var was defined as the difference between monthly maximum and minimum

temperature (i.e., mean diurnal range; bioclim 2), averaged over the two months preceding peak flowering or following the end of winter. Data management and summary statistics were performed with the packages included in the {tidyverse} suite.

Statistical analysis

The relationship of range size, thermal performance breadth and thermal elasticity with thermal variability – The relationship of range size, thermal performance breadth or trait elasticity in response to thermal treatments, and thermal variability was tested using generalised linear mixed models based on Markov Chain Monte Carlo techniques with the 'brm' function of the package {brms} (Bürkner 2017). Prior to analysis, the distribution of variables was checked by visual inspection of histograms with the function 'scatterplotMatrix' {car} (Fox and et al. 2018). Median elevation (Med_Elev) exhibited skewed distributions; Med_Elev and Temporal_Var.Wi where $\log_{10}$-transformed and Spatial_Var.Wi was square-transformed. Since (multi-) collinearity can be problematic in regression-type analysis, function 'vif' {usdm} (Naimi et al. 2014) was used to calculate the variance inflation factor (VIF) and 'vifstep' was used to remove predictor variables considerably correlated (VIF>3), which resulted in the discard of Spatial_Var.Wi and Temporal_Var.Wi. Finally, since environmental descriptors based on the timing of flowering and end of winter were highly correlated, and the latter removed from the dataset, we generalized the terminology of the remaining predictor as temporal and spatial thermal variability.

A first model had elevational range size (IQR_Elev) as dependent variable, and spatial and temporal thermal variability as predictors. Secondary models had the same independent variables, but the dependent variables were thermal performance breadth, elasticity or the absolute optimum of thermal performance as an estimate of thermal specialization ($|X_{opt}|$). Since RDPI is bounded between 0 and 1 (in our dataset min = 0, max = 0.5) and showed right-skewedness, we modelled it as a zero-inflated-beta distribution (to account for true 0s) or as a true beta after data transformation $RDPI' =$

$\frac{RDPI(N-1)+0.5}{N}$ (Smithson and Verkuilen 2006). Since both methods were equally good in predicting RDPI based on plots by 'pp_check' function {brms}, we selected the beta distribution on transformed data for final analysis in order to have a simpler model assuming that the 0s are not coming from different processes, but are mostly an approximation issue. Transformed data ranged from 0.00012 to 0.5. The random effects allowed variation in intercept for the crossed effects of trait, species relatedness, and thermal environment.

All analyses and figures were made using the statistics software R v. 4.0.2 (R Core Team 2014). Continuous predictors where centred (mean = 0 and scaled to unit variance) with the base function 'scale'. When not mentioned differently, mixed-effects models were performed with student distribution to improve robustness, and species relatedness was accounted by a variance-covariance matrix. Information on species relatedness came from a phylogeny produced based on several dozen chloroplast genes (Patsiou et al. 2020) and was pruned to species included in this study with the function 'treedata' of package geiger (Harmon et al. 2008). The final matrix was obtained with function 'vcv' {ape} (Paradis and Schliep 2018) and specified within the 'cov_ranef' setting in brm. Significance of Bayesian mixed-effects models was based on 90% credible-intervals (CI90), since they are more stable for Bayesian statistics as suggested by Kruschke (2014). Values were drawn from four independent parallel chains, where burn-in, number of iterations and thinning interval, as well as maximal tree-depth and adaptive delta were adjusted for each model to have an effective sampling size (ESS) of at least 1000. Calculations were performed at sciCORE (http://scicore.unibas.ch) scientific computing centre at the University of Basel.

The relationship of thermal elasticity with thermal performance breadth, and a trade-off in elasticity to frost and heat – Next, we tested for a positive relationship between trait elasticity and performance breath. In a first model, RDPI (square-root transformed and centred to mean = 0 and scaled to unit standard deviation) was the dependent variable and thermal performance breadth was the independent

variable. A second model tested whether RDPI changed with the location of the thermal optimum on the axis of thermal treatment (|X_{OPT}|).

Finally, to test for an association between elasticity to frost and elasticity to heat, frost elasticity was modelled as the dependent variable and heat elasticity as independent variable. Heat elasticity was square-root transformed, while frost elasticity was transformed by the formula $Frost.RDPI' = \frac{Frost.RDPI(N-1)+0.5}{N}$ and modelled assuming a beta distribution. Because of the special behaviour of thermal resistance compared to the rest of the eco-physiological traits and its relevance in a thermo-biological context, a second analogue model predicting $Frost.RDPI'_{resistance}$ dependent on $Heat.RDPI_{resistance}$ (square-root transformed and centred) was specifically performed.

Phylogenetic signal in range size, thermal variability, and physiological performance – Analysis on phylogenetic signals was performed using the 'phyloSignal' function in {phylosignal} (Keck et al. 2016). Three different measures of phylogenetic conservatism were tested: Moran's *I*, Bloomberg's *K* and Pagel's λ. A Moran's *I* of 0 means that species resemble each other as predicted under Brownian motion (BM); if $I < 0$, species resemble each other less than predicted under a Brownian motion model, and if $I > 0$, related species are more similar. Bloomberg's $K = 0$ indicates no phylogenetic signal, $K = 1$ suggests that trait distribution follows BM, and $K > 1$ indicates stronger similarity among closely related species. Similarly, Pagel's λ values range between 0, implying no phylogenetic signal, and 1, when a trait evolves under BM. *P*-values were calculated on a total of 10'000 permutations. To test for changes and depth of autocorrelation, we calculate Moran's phylogenetic correlograms using the function 'phyloCorrelogram' from the same package. Significance was assessed using 1'000 bootstrap replicates to estimate the 95% confidence interval (CI) of the correlation. CI curves not overlapping with 0 were considered significant.

RESULTS

The relationship of range size, thermal performance breadth or thermal elasticity with thermal variability

A first analysis tested for a relationship between elevational range size and thermal variability (Tab. 1). Elevational range-size was positively associated with spatial thermal variation of species occurrence but not with temporal variability in the thermal regime. However, neither thermal performance breadth nor thermal elasticity were positively associated with spatial variation in the thermal regime, with a probability of being positive of 66% and 64%, respectively. Thermal elasticity showed a significant negative relationship with temporal thermal variability, with a probability of 97%. In contrast, thermal performance breadth failed to show an association with temporal thermal variability, with a 76% probability of being positive. The absolute value of the optimum of thermal performance as the dependent variable also revealed no association with spatial variability in the thermal regime but a positive one with temporal variability. To summarise, larger elevational range size was associated with higher spatial but not temporal temperature variability, and larger trait elasticity in response to thermal regimes was, against predictions, associated with less temporal variability in the thermal regime as the species experiences it in nature.

The relationship of thermal elasticity with thermal performance breadth, and a trade-off in elasticity to frost and heat

Trait elasticity in response to experimental temperature was not related with thermal performance breadth, with a probability of 87% of being negative (CI90: [-0.162; 0.047], Tab. 2). However, trait elasticity declined with an increasing absolute thermal optimum of performance, with a strong probability of being negative (-0.046, CI90: [-0.096; -0.0003]; Fig. 2A, Tab. 2); species that are less plastic do better under extreme conditions, suggesting that they are more specialized.

Thermal elasticity in response to frost co-varied positively with thermal elasticity in response to heat (Fig. 2B, Tab. 3, 0.257, CI90: [0.196; 0.318]). When leaf thermal-resistance was analysed separately, a negative association between elasticity to frost and heat was detected (-0.222, CI90: [-0.388; -0.056]; Fig. 2C, Tab. 3).

Phylogenetic signal in range size, thermal variability, and physiological performance

The phylogenetic signal of environmental variables and thermal physiology are summarized in Table 4. The range of elevational occurrence did not show an effect of species relatedness neither in geographical nor in climatic (i.e. spatial variability) terms. However, the temporal thermal variability across the range was significant with an autocorrelation going back to 20 Mya (Supplementary material A2). Aspects of physiology showed little evidence of conservatism. A trend for a phylogenetic signal was observed for thermal-optima (autocorrelation going back approx. 10 Mya; not supported by *K*) and for elasticity in a few specific traits in some thermal environments (leaf dissection index$_{\text{mild-frost}}$, not supported by *K* and, leaf thermal resistance$_{\text{mild-heat}}$ not supported by λ; Supplementary material A2).

DISCUSSION

Past studies in ecology and biogeography predicted a positive association between climatic variability and climatic niche-breadth because of selection favouring more generalist genotypes and/or more plastic genotypes (Bradshaw 1965, Brown 1984). Our analysis focused on around 100 Brassicaceae species of the central Alps and revealed only partial support. Elevational range size was associated with spatial variability in temperature. However, spatial variability was neither related with the maintenance of thermal performance across experimental treatments, nor with trait elasticity in response to thermal treatments. On the contrary, we found that trait elasticity decreased when the realized variability between daily minima and daily maxima increased in areas where the species

occurred. In line, no strong link was found between elasticity and performance breadth, but elasticity decreased in species having optimal performance far from mild conditions (i.e., closer to cold or heat extremes). Evolution of thermal elasticity was not constrained by shared history and in general, no constraints in plasticity to frost *versus* heat were found except for thermal resistance. Results are discussed in the context of ecological thermal specialization and consequences for range size.

Factors related to range size

Our results indicated that elevational range size (i.e., the range of elevation where the species was found) is related to spatial thermal variability (i.e. the differences in mean temperature). This is not surprising since mean temperature was documented to change gradually along an elevational gradient with a mean of 0.5 K 100 m^{-1}. However, temporal variation (diurnal temperature range) was not associated with range size, suggesting that a wider realized thermal niche is not necessarily associated with increased daily temperature variability. Still, this negative result is in line with the greater diurnal temperature range that characterizes the high-mountain climate (Körner 2003, Supplementary material A4).

Two other hypotheses about a link with spatial variability were not supported by our data. Thermal performance breadth was not wider in species occurring at sites in which there was a more variable mean temperature. Furthermore, trait elasticity was also not greater in species covering over their distribution more thermal variability; only range size showed such a relationship. The two non-supportive results provide indirect evidence that elevational range size is not caused by species generally having wider performance curves over temperature regimes or by being more plastic. The lack of relationship between spatial variability in temperature and thermal performance breadth is in contradiction with classical theory, which predicts greater physiological flexibility for species in fluctuating environments (Janzen 1967; Alpert and Simms 2002; Ghalambor et al. 2007) and broadly thermal-adapted organisms in fluctuating environment (e.g., climate variability hypothesis (Stevens

1989), elevational Rapoport's rule (Stevens 1992)). The lack of support seems strong given how measuring was done. Our plant material came from an elevation typical for each of the plant species involved. Therefore, we can assume that the plants represented a fair fraction of the genetic makeup of each of the species and the phenotypic trait space each of the species occupies. Departing from this aspect of the study design, we can say that it is apparently not an inherent feature of a species, of each population and of most of its genotypes to show thermal performance breadth or high trait elasticity and therefore cover a wider range of thermal conditions across the species range. Based on our results, it seems more likely that a wide elevational range is achieved by climate adaptation, which seems to vary in its extent across species.

Another prediction, namely that thermal performance breadth would be associated with trait elasticity, was not supported either. Similarly, comparisons between high- *versus* low-elevation species detected negative relationships between niche breadth and plasticity across different abiotic components (nutrients, light, and moisture) indicating lower plasticity for generalist species (Dostal et al. 2017). Even if our results were not able to describe a non-null effect within the 90%CI, the negative trends we found point in the same direction. The recurrence of the phenomenon on several abiotic factors, across different species or within the same evolutionary context, suggests that a generalist strategy is not connected with greater phenotypic plasticity.

An interplay between diurnal thermal variability, trait elasticity and thermal optimum

Our results demonstrated a connection between short-term temporal fluctuations in temperature as they occur across species ranges and trait elasticity. Thermal-elasticity was negatively related with thermal variability occurring on a daily basis. The fact that strong daily variation did not select for enhanced thermal elasticity is not surprising because the time interval is very short for a phenotypic response in traits that we measured here. Interesting is that the relationship was negative, meaning

that a wider daily amplitude of thermal conditions selected for less responsive trait expression to thermal treatment, or in other words, for more robustness in trait expression.

Our analysis also suggested that phenotypic plasticity was associated with the thermal optimum. Elasticity decreased when the thermal optimum of a species deviated from generally mild conditions, towards the regular occurrence of either frost or heat. In other words, species adapted to mild conditions had greater plasticity, and those adapted to extremes had lower plasticity. The result is in line with finding by others. A meta-analyses supported an association between low tolerance and specialization in animals (Sunday et al. 2011). Other work reported lower in plasticity to be associated with an increase in baseline thermal tolerance (Kelly et al. 2013; Heerwaarden et al. 2016; Gilbert and Miles 2019). Our results are in line with these patterns and generalise the phenomenon by an extension to plants species, indicating that plasticity may be beneficial for species that have not acquired optimal adaptation to cool (or warm) conditions. Consequently, along an elevational gradient, we may observe specialized species (i.e., lower plasticity, optimal performance under thermal-extremes) where daily thermal-variability is considerable and generalist species (higher plasticity, doing best at mild-conditions) in most stable thermal-environment.

Constraints and evolutionary conservatism

Evidence for constraints in thermal plasticity (to frost *versus* heat) were inconsistent. Generally, higher elasticity in response to regular heat was associated with higher elasticity to regular frost, leading to generally more or less plastic species. The result is to some extent in line with the negative relationship between general plasticity and thermal specialization. When species do better under thermal extremes, they are less plastic, and this seems to work independent of the thermal cue. In contrast, species that prefer thermal averages are more plastic to thermal cues of low and high temperatures. The finding supports a generalist-specialist trade-off.

However, the sign of the relationship between elasticity in response to regular frost and elasticity in response to regular heat was reversed for thermal resistance. Growth under thermally slightly challenging conditions can induce increased resistance, known as acclimation or hardening. It seems that plants either show an increased hardening response to frost, or an increased hardening response to heat, but the two trade off against each other. What has been shown so far in Brassicaceae is that there is cross acclimation to frost and heat, that frost during growth increases subsequent frost and heat resistance, and that heat during growth also increases subsequent heat resistance but also – to a reduced extent – frost resistance (Wos and Willi 2018). Results found here imply that induced resistance, potentially including cross resistance, is constrained by a plant species being either generally acclimation responsive to frost or heat, but not both.

Across the environmental descriptors, inter-quantile range and spatial thermal variation did not displayed consensus for phylogenetic conservatisms. Across the thermal physiology descriptors, marginal support for phylogenetic conservatism was given to thermal optima, which was supported with intermediate values by λ and I but only as a trend from K. The very deep autocorrelation in diurnal temperature range and the relatively recent one for thermal optima suggest that evolution through optimality in performance follows adaptation for highly or low fluctuating environments. Similarly, the recent autocorrelation for elevation suggests that adaptation to climatically varying environment preceded and helped the colonization along the Alps. All together, these patterns support what was discussed above: diurnal temperature range (which is phylogenetically constrained) is a critical environmental filter, requiring thermal-specialization and canalization in thermal plasticity.

While physiology and especially environments displayed a strong signal of conservatisms, trait plasticity was generally weakly constrained by shared history. Elasticity different from zero was recorded in only few traits and for only specific index. Studies addressing phylogenetic signal for plasticity are scarce. In a recent work on amphibians, Relyea et al (2018) tried to explore phylogenetic

conservatisms in plastic traits across life-history variables resulting in only few traits exhibiting significant effect. Our lack of phylogenetic signal, which may reflect the limitations of this study (e.g., tree was based only on few species from the entire family and traits plasticity assessed for only three main thermal regimes), seems to fit in a more general pattern where plastic response is less constrained in its evolution supporting hypothesis of great evolutionary flexibility.

CONCLUSION

The expectation of increased thermal performance breadth or thermal elasticity in species occupying a wide spatial distribution is not supported in the current study. In fact, while a high correlation between the extent of the elevational distribution of Brassicaceae and the variation in average temperature was identified; the latter showed no link either with thermal performance breadth nor with thermal elasticity. However, thermal elasticity was reduced when species had a higher diurnal temperature range where they occurred. A negative association between elasticity and thermal-optima (i.e., thermal-specialization) was also found by disentangling the link between thermal-elasticity and thermal-performance. As a result, range-size along an elevational gradient seem mainly driven by two opposing strategies: thermal generalist (optima at mild conditions, with increased thermal-elasticity) or thermal specialist (optima for thermal-extremes, with lowered thermal-elasticity). Moreover, colonization of highly thermally heterogenous landscapes seem primarily limited by phylogenetic constraints rather than constraints in the evolvability of plastic responses. Those findings suggest that variation in range size can be explained by an interplay between adaptation to thermal heterogeneous environments and thermal specialization.

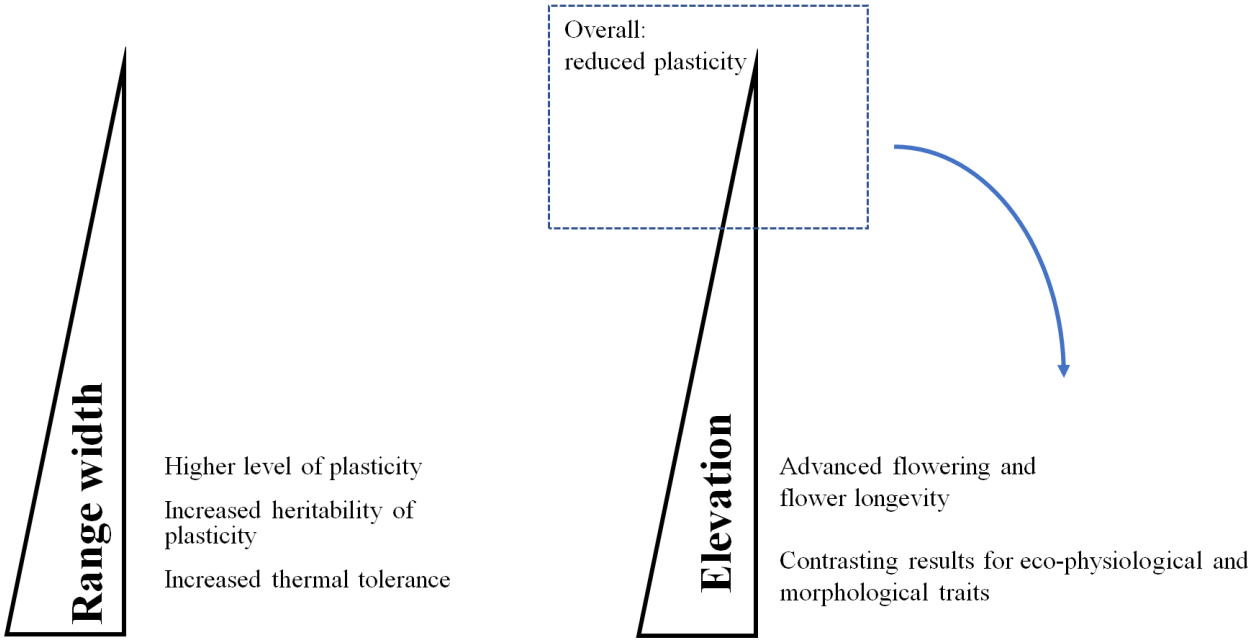

Figure 1: Summary of variation of plasticity depending on species range width (*left*) and elevation (*right*; based on transplant experiments).

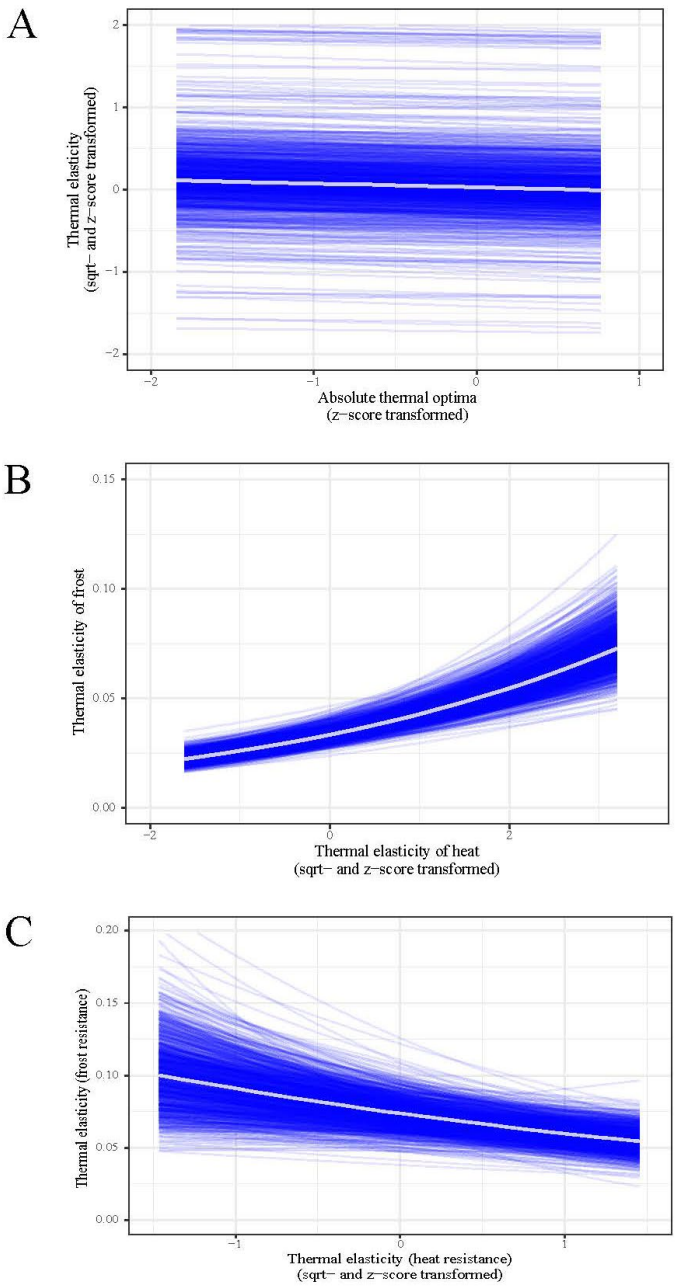

Figure 2: *A*. Impact of thermal optima (X_{OPT}) on thermal elasticity in eco-physiological traits. *B*. Relationship between RDPI under frost and heat conditions. *C*. Relationship between RDPI for frost- and heat-resistance. Each line represents different draws (of 1'000 model runs) of conditional effects of the model and white line represent the median.

Table 1: Mixed-effects model describing the relationship between geographic range size (IQR), thermal performance and thermal-elasticity (RDPI).

	Intercept	Spatial variation	Temporal variation
IQR elevation	-0.018	**0.753**	-0.067
90%HDI	[-0.247, 0.224]	**[0.632, 0.880]**	[-0.210, 0.082]
Thermal performance breadth	**0.630**	0.012	0.023
90%HDI	**[0.563, 0.709]**	[-0.035, 0.062]	[-0.029, 0.073]
Thermal elasticity (RDPI)	**-2.570**	0.010	**-0.053**
90%HDI	**[-3.532, -1.304]**	[-0.035, 0.053]	**[-0.100, -0.008]**
Thermal performance optima	**0.861**	0.051	**0.469**
90%HDI	**[0.539, 1.190]**	[-0.193, 0.299]	**[0.217, 0.717]**

Value represent the posterior mean and the 90% credible interval (90CI). Significance is given when the 90CI is non-overlapping with 0. Significant predictors are highlighted in **bold.**

Table 2: Mixed-effects model describing the effect of thermal-elasticity on thermal-breadth and optimal temperature. Thermal performance breadth was log_{10}-transformed, RDPI was square-root transformed and all the predictors and response variable were mean-centred and variance-scaled.

	Intercept	Thermal performance breadth
RDPI	0.021	-0.041
	[-0.532, 0.508]	[-0.123, 0.040]

	Intercept	Thermal optima (XOPT)
RDPI	0.067	**-0.046**
	[-0.526, 0.716]	**[-0.096, -0.0003]**

Value represent the posterior mean and the 90% credible interval (90CI). Significance is given when the 90CI is non-overlapping with 0. Significant predictors are highlighted in **bold.**

Table 3: Mixed-effects model for relationships between trait elasticity (RDPI) to frost and elasticity to heat. Thermal elasticity (RDPI) for mild-heat was square-root transformed and centred to mean 0 prior to run analysis. In complete model (i.e. including all the traits), random intercept was modelled based on traits within species. In contrast, resistance only (i.e., only thermal-resistance was used), random intercept was modelled for species relatedness.

		Intercept	RDPI (mild-heat)
Complete	RDPI (mild-frost)	**-3.363**	**0.257**
		[-3.508, -3.210]	**[0.196, 0.318]**
Resistance only	RDPI (mild-frost)	**-2.536**	**-0.222**
		[-2.803, -2.280]	**[-0.388, -0.056]**

Significance is given if the 90% confidence interval (CI) is non-overlapping with 0. Significant predictors are highlighted in **bold.**

Table 4: Phylogenetic signal for environmental variability and thermal performance

	Moran's *I*	Bloomberg's *K*	Pagel's λ
Geography			
Elevation range size	-0.017	0.103	0.000
Thermal environment (Climatic)			
Spatial termperature variability	-0.034	0.127	0.000
Temporal temperature variability	**0.138** ***	**0.330** ***	**0.532** ***
Thermal physiology			
Absolute thermal optimum (XOPT)	**0.071** *	0.170 (.)	**0.313** *
Thermal performance breadth	-0.018	0.161	0.000

P-values are based on 10'000 permutations. $P > 0.1$ (.), > 0.05 *, > 0.01 **, > 0.001 ***. Numbers in **bold** highlight significant results

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CHAPTER 3

Divergent adaptation to climate in Brassicaceae species differing in elevational distribution

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Acknowledgements

We thank Lea Bona, Camilla Jenny, Adrian Möhl, Ramon Müller, Jens Paulsen, Florian Schreier, and Daniel Slodowicz, for collecting seeds in the field. Georg Armbruster, Jens Paulsen, Marco Barandun and Fabian Heussler helped with the setting up of the field sites. Georg Armbruster , Olivier Bachmann, Markus Funk, Kay Lucek, Michela Meier, Antoine Perrier, Susanna Riedl, helped with sowing seeds and fruitful discussions. Adrian Metry, Amos a Marca, Bianca Modespacher and Nicolas Feigenwinter helped with plant measuring. The ETH Zürich (Institute of Integrative Biology) and the municipality of Haldenstein provided access to field sites. Finally, we would like to thank all the field botanists that contributed with occurrence data to the InfoFlora database.

ABSTRACT

Past research has pointed to temperature as the most important driver of species range limits. However, it is unclear what the shape of lifetime performance on the temperature gradient under natural conditions is, what descript of temperature the most influential is, and how aspects of lifetime performance are affected by it. In the current work we investigated the role of thermal adaptation in shaping elevational range limits by a transplant experiment involving 30 Brassicaceae species differing in their elevational distribution. Plants were grown in five transplant sites (from 600 to 2000 m) along a 3 km transect in the central Alps. We assessed growth rate, survival and reproductive output and we tested whether they vary based on environmental conditions and the elevation of origin of species. Furthermore, we included lifetime performance and we tested for climate adaptation both as *home-away* and *local-foreign* effect. Our results indicate that growth and survival depend on environment and origin, i.e., alpine species are fast-growing, but their survival probability is lower. Lifetime performance decreases with increasing distance between transplant site and origin, indicating that species are adapted to the macroclimate where they occur. However, we found no direct evidence for thermal adaptation since for example no specific link with temperature and mortality depending on origin could be made. We conclude that differences in elevational distribution among species may be driven by adaptation involving growth, survival and a likely allocation trade-off between them.

Key words: Climate adaptation - Maximal growth rate – Maximal temperature - Phylogeny – Thermal adaptation – Survival rate – Range-limits

INTRODUCTION

Among the many potential components of the niche, temperature has always been thought to be among the most important in determining species distribution (MacArthur, 1972; Sexton et al. 2009). However, the mechanistic effect that temperature has on performance in nature is not well understood. What makes the matter more complicated is that the effect that temperature has may depend on the way species are differentially adapted to climate. This lack of knowledge is also linked with several other open questions ranging from the extent to which species are adapted to macro-climatic conditions of native sites, to the best descriptors of the thermal niche of species (Körner and Hiltbrunner 2018).

Many phenomena point to a key role of temperature in shaping species distribution. In gardening or agriculture, the concept of the "hardiness zone" has been developed to describe climatic areas suitable for the growth of particular plants. Past seminal contributions based on correlative or experimental approaches have translated these observations into empirical evidence (Iversen 1944; Dahl 1951; Janzen 1967), opening the way for the joint study of thermo-biology and species distribution. Despite some criticism for its over-reliance on correlational techniques (Samways et al. 1999; Gaston 2003; Parmesan et al. 2005), the relationship between geographical species distribution and thermal tolerance has been frequently reported (e.g., Addo-Bediako et al. 2000; Bozinovic et al. 2011; Sunday et al. 2011, 2019). Furthermore, the physiological consequences of temperature on organisms is well-known for a wide range of taxa (e.g., Somero 2005; Cossins 2012; Sakai and Larcher 2012). In the past decades, climate change promoted an increased interest in predicting species responses to temperature and range shifts (e.g., Thomas et al. 1999; Walther et al. 2002; Parmesan and Yohe 2003; Menzel et al. 2006; Parmesan 2006).

Among the studies focusing on range limits (latitudinal or elevational), it has been common to assess components of individual performance along the abiotic gradient *in situ* or under experimental conditions and relating them to the abiotic stressor. In latitudinal studies, patterns

frequently observed are higher fitness for local genotypes (e.g., Agren and Schemske 2012), performance reductions near or beyond range edges (e.g., Stanton-Geddes et al. 2012; Vergeer and Kunin 2013), including a reduction in growth rate (e.g., Li et al. 1998; Kollmann and Bañuelos 2004). Similar patterns were described for elevational gradients. Low-elevation species transplanted to higher elevation showed reduced growth and decreased survival (Angert and Schemske 2005; Angert 2006; Bastida et al. 2015; Hämälä et al. 2018), while high-elevation species or ecotypes transplanted to low elevation showed increased mortality, reduced fecundity, slower development and lower biomass (Angert and Schemske 2005; Angert 2006; Montesinos-Navarro et al. 2011; Hämälä et al. 2018). Beside this general overlap in findings, other studies found only marginal or no effects of temperature on performance (e.g., Vergeer and Kunin 2011), or increased in growth when high-elevation plants are subjected to low elevation conditions (e.g., Mächler and Nösberger 1977; Ran et al. 2013), or no effect of transplant in survival (e.g., Bastida et al. 2015).

Part of the inconsistent patterns may be the result of the design of several transplant experiments where, for example, they were too short to capture climate extremes or negative effects of chronic exposure to thermal-stress. An additional problem arises in studies that explicitly account for temperature, since the way it is recorded is highly variable: sometimes it is measured *in situ*, sometimes it is extrapolated from nearest meteorological stations or long-term climate data. The latter approaches bear the risk of missing microclimatic effects that can only be depicted by the *in situ*-tracking of temperature. Microclimatic variations can be important, e.g., comparisons of soil and weather station records resulted in deviation of up to 10 K (Graae et al. 2012) and similar values apply at the individual level (Scherrer and Körner 2010). In parallel, microsite exposure has been shown to affect frost exposure (frequency, length and severity) and the length of growing season (Jordan and Smith 1995), with likely consequences for thermal adaptation. These observations lead to two consequences. The first is that organisms may be subject to benign temperatures even when extrapolated or monthly averages predict harsh conditions; the other is that species occurring at high-

elevation can have thermal environments close to those expected for low elevation. As a consequence, microclimatic effects are not subtleties, and should strongly impact how we test for thermal adaptation in the species (its ecological and evolutionary significance): is an alpine plant really adapted to a lower temperature optimum? Or does it simply occupy a specific microclimate? And more generally, to which extent should species be differentially adapted and respond to macro-climatic conditions?

These questions can be further magnified if we consider that organisms are not solely limited in their distribution (e.g., high *vs* low or north *vs* south), but they also differ in the extent of their range. The range-size variation effect is often neglected in studies, but it can have profound implications since species that have larger geographic ranges are expected to have greater tolerance to a wider range of environmental conditions (Brown 1984). As a consequence, species that have the same origin, but differ in their range-size, can have different thermal tolerances, which may lead to different responses.

Here we studied the extent to which temperature affects the shape of performance along an elevational gradient and contributes to the divergent distribution of plant species over the gradient. Analysis were performed in a macroevolutionary framework. Our study involved 30 Brassicaceae species occurring in the central Alps of Europe, with a median elevation of occurrence ranging from 400 to 2750 m a.sl. Under controlled conditions, divergent selection acting on the elevational gradient has been identified in Brassicaceae, with selection at high elevation favouring fast development under warm conditions and selection at low elevation favouring cold-tolerance (Maccagni and Willi *submitted*). These were also the traits found to be most discriminating between high- and low-elevation species, despite other differences, including small size of high-elevation species. More generally, strong differentiation in thermal responses seem to be the predominant differentiating characters betwen low- *versus* high-elevation species. Here we raised plants across an elevational gradient in nature (from 600 to 2000 m a.s.l.) in central Alps, with 5 transplants sites across the

gradient. Temperature was recorded above the ground, and growth, survival and lifetime performance recorded at the level of plants.

The following questions were addressed: i) Do the local environment and differences in origin (elevation) of species affect survival and growth? ii) What aspect of the general temperature regime influences survival and maximal growth rate most? Is there variation between origin? iii) Are species adapted to climatic conditions that prevail at their commonest elevation of occurrence? iv) Is there variation in the relative contribution of different components of performance (growth rate, survival, and lifetime performance) to any overall home advantage? Does it differ between low and high elevation?

MATERIAL AND METHODS

Choice of species and sampling

Thirty species belonging to the Brassicaceae family and naturally occurring in the central European Alps, from the colline to the alpine life zone,were selected. They were part of two species-rich tribes occurring in the Alps (Cardaminae and Arabideae) and had similar ecological requirements (i.e. Landolt's moisture indicator values between 2 and 4), but they differed in elevational distribution. The species list is available in supplementary material A1. Seeds were collected from March to September during the years 2015-2017 at two different sites in the Swiss Alps located at least 50km apart from each other, and preferentially from different biogeographic regions. The sites were at the most common elevation for each species. Seeds sampled from separate plants in the field were stored separately in paper bags (80 g m^{-2}, 60 × 90 / 12 mm, ELCO AG, Brugg, Switzerland) under cold (4 °C), dark and dry (added silica gel) conditions until sowing.

Sowing, pre-growth conditions and transplant site

Design – The experimental design involved the raising of 30 species, each represented by 2 populations and 5 plants from which seeds were collected per population in the field, i.e. 10 seed families per species. The experiment was split into 5 transplant sites at different elevations, with two blocks/replicates per site, and each block containing the 10 seed families per species. The final design resulted in 600 individuals *per* site and 3'000 in total (30 species × 10 seed families × 2 blocks/replicates × 5 sites = 3'000 individuals). The sowing was done in 5 rounds, one for each transplant site, such that when seedlings were brought out to a transplant site in late summer to fall, average temperature conditions were comparable.

Sowing and pre-growth conditions – Seeds of each seed family were haphazardly selected. Seeds were incubated in 500µl of gibberellic acid solution (500ppm, Merck KGeA, Dornstadt, Germany) for 1 week in dark and cold (4°C constant; Climecab 1400 Kälte 3000 AG, Landquart, Switzerland) to trigger synchronous germination. Then seeds were sown by random spatial order in multipot-trays (0.2L, 28 pots per tray 6×7cm, Quick-Pot QP; gvz-rossat.ch, Otelfingen, Switzerland), filled with a mix of soil (bark compost, peat and perlite; Aussaat- und Pikiererde; Oekohum, oekohum.ch, Herrenhof, Switzerland) and sand (0-4mm) in a ratio of 2:1; and transferred in growth chambers (MobyLux GroBanks, CLF Plant Climatics, plantclimatics.de, Wertingen, Deutschland). All growth chambers were located inside a PlantMaster (CLF, Plant Climatics, plantclimatics.de, Wertingen, Deutschland) with controlled humidity and temperature. Trays were kept at 15/18 °C night:day, 75% relative humidity (RH), light:dark 8:16 h at 200 µmol m^2 s^{-1} (fluorescent white lamps and red-LED). After 3 weeks, excess seedlings were used to fill pots without any germination. In week 4, light was gradually increased to maximal capacity (400 µmol m^2 s^{-1}, by steps of 50 µmol m^2 s^{-1} every second day) to acclimate plants to field conditions. Plants where moved to the transplant sites at 2- to 4-leaf stage.

Transplant sites – Five different sites (Tab. 1), representing different elevational life-zones, were selected along a 3-km transect on a south-facing slope in Calanda region (Switzerland; Lat. 46.875, Long. 9.501), in the central Alps: colline ("Im Bofel", 600 m a.s.l.), montane ("Arella", 1'000 m a.s.l.), mid-montane ("Nesselboden", 1400 m a.s.l.), alti-montane ("Oberberg", 1'600 m a.s.l.) and subalpine ("Gruoben", 2'000 m a.s.l.). Multipot-trays with germinated plants were moved to the field sites in fall, when predicted daily mean temperature based on the nearest meteo-station were dropping to around 10 °C, starting with the site on the top and ending on the bottom (14/08/2018, 12/09/2018, 20/09/2018, 26/09/2018, 10/10/2018). The trays were buried into soil and arranged in two spatially separated blocks, each composed of 11 trays arranged in 2 parallel rows. During the first week, trays were covered by a shading net and watered twice a week with 20 L of water per block. Then the netting was removed and watering reduced but maintained during part of the first fall to compensate for the reduced substrate volume in the pots and high evaporation when needed. At each site, temperature was recorded 5 cm above the soil surface ("micro-climatic" temperature) every 15 min (Thermologger, TOMST s.r.o., Prague, Czech Republic) by 4 loggers installed above randomly selected empty pots and spit across the two blocks.

Trait assessment

Growth and survival – Plant growth and survival were monitored from fall 2018 to fall 2019. To assess plant growth, the number of leaves (> 2mm, green and non-senescent) of individual plants was counted every week during the first month after transplanting, and then every two weeks until fruit production occurred. Leaf number (NLEA) was used to model relative growth rate as $RGR = \frac{(NLEA_{T2} - NLEA_{T1})}{NLEA_{T1}\, Time}$, where $NLEA_{T1}$ and $_{T2}$ represent the number of leaves recorded on two subsequent dates of counting and time was the number of days between T1 and T2. The highest value observed of RGR was then used to define the maximal relative growth rate (MRGR). Survival was recorded as a binary outcome (i.e., 0: alive, 1: death) once a week for the entire survey period except when sites

were snow-covered and inaccessible. Mortality was assigned when plants were completely dry, with no more green tissue neither in apical nor lateral buds. Mortality occurring over the first week after transplant were discarded to prior analysis, assuming that it occurred due to transplanting rather than environmental effects. The remaining time-values were standardized across sites to have the same number of weeks (same maximal survival-age across sites).

Lifetime performance – Reproductive output (REPRO) was used as proxy of performance, and was calculated on the level of the species-block-transplant site level. REPRO was calculated by the number of fruits (i.e. siliques) produced at the time when the first ripe fruit was scored. Inflorescences were collected in paper bags, dried at 65 °C for 48 h for storage, and subsequently fruits were counted. For big inflorescences (> 50 fruits *per stem*) with homogenous fruit set, fruit number was estimated by counting the number of fruits along a 5 cm fragment and extrapolating for the entire stem length; if multiple stems where produced, the same procedure was applied independently to each of them and values were summed up.

REPRO was then used to estimate life-time performance for each species-block-transplant site combination in the two reproductive seasons, by using the 2019 values and extrapolating for 2020. First, we calculated the fraction of individuals able to reproduce (FRAR), calculated as the ratio between the number of individuals which reproduced in 2019, divided by the number of individuals alive in spring 2019. In parallel, mean fruit production was calculated across plants that survived initial transplanting. REPRO 2019 has thus been defined as the average fruit production multiplied by the number of individuals which reproduced. Second, REPRO 2020 was extrapolated as follows: first, by estimating the number of potential reproductive individuals, multiplying the number of living individuals in spring 2020 by the value of FRAR. Then, by assigning them the mean reproductive value obtained in 2019, by block-specie-transplant site combination. Third, mean REPRO 2019 and extrapolated mean REPRO 2020 were then added with each other, resulting in the cumulative production of fruits over the two seasons for each block-species-transplant site combination.

Statistical analysis

Overall effect of macro-environments and origin on growth and survival

Growth and survival – The effect of the environment (elevation of transplant site), elevation of origin (median elevation of species distribution) and range size was tested via a Bayesian mixed-effects model implemented with the 'brm' function {brms} (Bürkner 2017). Both environment and elevation of origin were treated as continuous variables. The effect of environment, elevation of origin, and range size on survival across the gradient was tested via a survival regression model. The model was again implemented within the brms package as mixed-effects model but using a Weibull family distribution (Fox 2001). Response variable was time of survival (in weeks after transplantation), and individuals were right-censored if they remained alive for the entire observation time. Predictors were mean centred to 0 and scaled to unit variance prior to analysis. The random part of the models included seed family within population and species, population within species, and species; for these, intercept and slope on environment was estimated. Since our dataset was composed both by non-therophyte and therophyte species (i.e., plants died after producing fruits), we run the model under three different scenarios to account for the potential bias in survival induced by reproduction. A first sub-model used the raw data (i.e., "complete"), a second sub-model was based on a subset which excluded all the therophytes (i.e., "therophyte removed") and a third model removed mortality to each therophyte which successfully reproduced, assuming mortality was independent of the environmental conditions (i.e., "therophyte-altered").

All analyses and figures were performed using the statistics software R v. 4.0.2 (R Core Team 2014). Data manipulation was performed with the {tidyverse} suite and time operation with {lubridate} package (Spinu et al. 2018). Where not differently specified, mixed-effects models were performed with Student's t distribution to improve robustness (i.e. reduces sensitivity to outliers) and species relatedness was accounted by a variance-covariance matrix. Information on species relatedness came from a phylogeny produced based on several dozen chloroplast genes (Patsiou et al.

2020) and was pruned to species included in this study with the unction 'treedata' of package geiger (Harmon et al. 2008). The final matrix was obtained with function 'vcv' {ape} (Paradis and Schliep 2018) and specified within the 'cov_ranef' setting in 'brm'. All the predictors and continuous response variables were centred to mean 0 and scaled to unit variance to improve model convergence, and median elevation of origin previously log-transformed (base 10) to improve normality. Posteriors were reported as median values, and significance evaluated as 90% credible-interval (CI90) of the high-density interval (HDI) and decision based on the probability of direction with the {bayestestR} package (Makowski et al. 2019). Values were drawn from four independent parallel chains, where burn-in, number of iterations and thinning interval, as well as maximal tree-depth and adaptive delta were adapted to each model to have at least 1'000 effective sampling size (ESS). Model convergence was checked by visually inspecting diagnostic plots and Rhat values. Calculations were performed at sciCORE (http://scicore.unibas.ch) scientific computing centre at University of Basel.

Most influential temperature predictor of performance components and effect of origin

In a next step, we tried to elucidate what aspect of temperature led to maximal growth rate or death. Aspects of temperature were calculated in the interval between the recording of the trait state and the 30 days preceding it, at the individual level, and subsequently pooled at the level of species within blocks. The temperature variables were minimum, median, median absolute deviation (i.e., MAD), maximum, no. of days with T > 35°C, < -3°C, cumulative heat > 35°C, cumulative frost < -3°C. Since (multi-)collinearity can be problematic in regression-type analysis, the function 'vif' {usdm} (Naimi et al. 2014) was used to calculate the variance inflation factor (VIF) and 'vifstep' was used to remove predictor variables highly correlated (VIF>10). Median temperature and number of days with T > 35°C were excluded for both maximal growth rate and death. According to VIF analysis, the number of freezing days was additionally removed for MRGR, and cumulative frost for the analysis of death. Species were then grouped in two classes based on their elevation of occurrence (threshold at 1400m):

colline-mid montane ("low") and subalpine-alpine ("high"). Then, an additive Bayesian mixed-effects models was built to test whether and which aspects of temperature, associated to which performance components, were able to distinguish between high and low elevation species indicating differential thermal-adaptation. Model was built under a Bernoulli response distribution, while predictors were the remain thermal-descriptors as additive terms. Random crossed effect were taxa and blocks.

Adaptation to macro-climate in alpine species and variation in relative contribution of different components of performance

Evidence for local adaptation can be detected by increased species performance at their own habitat (i.e., at high transplant site for alpine species, at low transplant site for lowland). This interaction will lead to test for variation in performance *at home* against *away*. This approach assumes that with increasing distance from home-site, performance will decline. The effect of the distance from elevation of transplant site to elevation of origin, (i.e., Δ-Elevation; negative values indicate transplanting to lower elevation, positive values to higher elevation) on lifetime performance was tested via mixed-effects model with 'brm' function. A first model tested for a linear and quadratic effect of Δ-Elevation, allowing for variation in slope and intercept for taxa and taxa within blocks. However, since higher- or lower-elevation species can be intrinsically biased (i.e., transplanted only up- or down-wards), Δ-Elevation was modelled in interaction with species origin. A second model tested for an effect of absolute Δ-Elevation (i.e., |Δ-Elevation|; higher values indicate transplant away from origin), range size and their interaction, assuming more generalist species can react differently). In both models, predictors were centred and scaled, and lifetime performance was centred and scaled across sites independently for each species-block combination.

However, Kawecki and Ebert (2004) suggested that the key comparisons in the testing of local adaptation should be between local and foreign genotypes within each habitat (i.e., testing whether at

higher site, alpine species (local) perform better than lowland species (foreign) and *vice versa*). For this purpose, lifetime performance was modelled by a mixed-effects model, where fixed effects were transplant site (as categorical variable) in interaction with plant origin (as continuous median elevation), omitting the main intercept. Analogue models were performed to test whether broadly occurring species differ in their response than species with narrower range (i.e., broadly occurring species maintain higher performance with increasing distance). For this purpose, each transplant site (categorical) was in interaction with range size and |Δ-Elevation| to correct for the distance from transplant site and origin. Analogue models were performed for maximal relative growth rate and survival probability. Survival probability represent the ratio of survivors over the entire period, calculated as the ratio between survival individuals on transplanted one (based on therophyte altered dataset). Values were calculated at species level independently for each block within site.

To test whether and how the relative importance of survival, growth and lifetime performance varies along the gradient, we performed a Dirichlet regression. Response variable were maximal relative growth rate, survival probability and lifetime performance, rescaled each in the range [0, 1] to have comparable contributions, and then corrected in order that the sum of the three estimate was equal to 1 (at species level, for each block within site). Predictor variables were environment, origin (and their quadratic terms) and the interaction, while varying intercept was allowed for the crossed random effect of species relatedness and block. Model was performed with 'brm' function with Dirichlet family distribution for the joint response variable.

RESULTS

Overall effect of macro-environment and origin on performance

Growth and survival – Maximum growth varied depending on transplant site (Tab. 2); it was lower at higher elevation, where there was a certainly existing negative effect of environment (-0.068). Maximum growth also varied with the elevation of origin of speices, in the opposite direction. High-

elevation species had faster growth, with a certainly existing positive relationship (0.089). The effect of range-size was - as a trend - positive (0.030, CI90%[-0.001, 0.060]; 95%), suggesting a tendency of broadly occurring species to be fast growing compared to narrowly restricted species. Survival probability was also affected by the elevation of the transplant site (in all datasets) and by elevation of origin (Tab. 2); however, differences in magnitude and direction existed based on how annual plants were treated. Elevation of transplant site had a being positive effect in the complete and reduced dataset, with similar magnitudes (0.104 and 0.115; 100%), indicating that an increase in elevation extended the lifespan. However, under the therophyte-altered model, the effect tended to be negative (-0.054, 99%), indicating that increase in elevation reduced overall lifespan. In conclusion, we learn that perennial species tend to have a longer lifespan at higher elevation. Elevation of origin of species was non-significant under the complete dataset, however it had a high probability of being negative both under the therophyte-altered and removed dataset (-0.183, 96% and -0.377, 99%). Across models, the pattern that emerged was that high-elevation species had a shorter lifespan compared to low-elevation species. Range size was overall non-significant, showing a 93% probability of being positive in the complete and altered dataset.

Role of temperature for growth and survival

Environmental thermal descriptors were able to distinguish between high and low elevation plants for thermal-requirement in maximal growth rate (Tab. 3). Within the 5 different descriptors, only the maximal temperature had a likely existing effect with a 97% probability of being positive, i.e., higher temperature associated to fast growth were likely to predict elevation of origin, with alpine species having better performance under warmer conditions. In contrast, mortality was unaffected by any of the five predictors (Tab. 3).

Adaptation to macro-climate in alpine species and variation in relative contribution of performance components

Distance from origin (*home-away effect*) resulted in a positive effect on lifetime performance and survival ratio (Tab. 4.1, Fig. 1). The effect of Δ-Elevation was probably existing with a 99% probability of being positive for the linear component and of 98% for the quadratic term. The effect of distance on lifetime performance was certainly existing, when looking at its absolute value (Tab. 4.2), but was unaffected by the extent of the range-size, which was limited to a positive trend (0.084, CI90%[-0.012, 0.180]). When we analyse the other components of performance, similar results applied for the fraction of survival, which responds positively to the increase in range size, which had a certainly existing effect with a 100% probability of being positive (Tab. 4.2). In contrast, maximal growth rate was unrelated to the variation in distance and/or amplitude of the species. Summing up, as the distance from the environment of origin increases, the lifetime performance and the probability of survival were reduced; while higher range-size buffer against negative effect of environment.

Local-foreign effects resulted in more controversial trend (Tab. 4.3, 4.4 and Fig. 2). At lowest site (600, 1000 m), the effect of origin was likely existing with a probability >98% of being negative; while at the highest site (2000 m), origin had a certainly existing positive effect, i.e., at low elevation, alpine species were outperformed by lowland plants, and the opposite applies at high elevation. On the other hand, in transplant site located at mid elevation, no origin was advantaged. Among other performance components, survival probability was not significantly different between high and low elevation species at common gardens located below 1600 m. At 1600 site, the effect of origin was certainly existing, with a 100% probability of being negative, suggesting that low-elevation species outperformed alpine ones. However, at 2000 m the effect was the opposite and origin had a certainly existing probability of being positive. Maximal growth rate differed significantly only within the 1000 m transplant site, where origin had a possibly existing positive effect with a 96% probability, indicating better performance for alpine species. Testing for range-size effect (Tab. 4.4) gave results

in line with the *home-away* effect. Lifetime performance differed from zero only at the 1600 m site, with a higher probability of being positive (97%). In contrast, survival probability differed between broadly and narrowing occurring species. At 600, 1600 and 2000 m there was a higher probability (> 95%) of an existing positive effect of range-size suggesting that species with wider range were able to buffer against environmental conditions far from what commonly experienced. Maximal growth rate was unaffected by range-size variation at any site. In general, the local-foreign comparison supports the home-away results but indicates that the variation in performance was not linear along the gradient, but rather leaded by the extremes.

Environmental gradient and origin influenced the variation in the relative contribution of life-time performance, survival, and growth rate (Tab. 5, Fig. 2). Results indicated that lifetime performance variation in comparisons to maximal growth rate, was negatively associated with environmental variation under linear term, and certainly existing as positive quadratic effect. Effect of origin was certainly existing with a probability of 100% of being negative, however, the interaction between environment and origin resulted in a certainly existing effect, with 100% of probability of being positive, i.e., alpine species under high-elevation environment had increased lifetime performance at the expense of reduced maximal growth rate. The relative variation in probability of survival compared to maximal growth rate, was affected by environment and origin. Linear and quadratic effect of environment were likely to exist, with a probability > 97% of being positive. Effect of origin was certainly existing with a probability of 100% of being negative. Therefore, interaction between origin and environment resulted in a non-significant positive effect.

DISCUSSION

Seminal work in biogeography indicated temperature as one of the most important determinants in shaping geographic species distribution. One of the questions is whether it is thermal adaptation that differs among species and causes their different distributions, and whether is it thermal adaptation

that fails at range limits. Here we tested the role of thermal adaptation and the extent to which it contributes to set the elevational range limits within an evolutionary framework, in 30 Brassicaceae species of central Alps. Our analysis indicate that growth rate and survival are affected by the immediate macro-climatic environment as well as by the climate they come from, here depicted by the median elevation species are found in the central Alps. Results indicate that Brassicaceae are adapted to the macroclimatic conditions prevailing where plants occur, but there seems to be no direct evidence with thermal-adaptation. For example, alpine species grow faster, especially when the climatic conditions are warmer, and there is no effect of temperature on mortality. However, differential allocation to growth rate seems promoting variation in lifetime performance suggesting potential cost-allocation trade-offs. Results are discussed in the context of adaptation across the elevational gradient.

Effect of origin and environment on growth and survival

Our data indicate that genetic and environment affect growth and survival. The maximal growth rate had a positive increase with elevation of occurrence indicating that high-elevation species are consistently fast growing than low elevation ones. Fast growth has been reported for species occupying rich soils, having an annual life-strategy or occurring in environments with lower levels of stress (Grime 1979; Pugnaire and Valladares 1999). Within the literature of alpine ectotherms, we have contrasting empirical evidence since some authors reported slow growth (Atkin and Day 1990; Körner 2003), while others indicated faster growth (e.g., Berner et al. 2004; Laiolo and Obeso 2015). The latter seem to being supported by modelling work, which reported season length as limiting factor in northern or upper range limits (Morin et al. 2007; Normand et al. 2009; Patsiou et al. 2020) suggesting that faster development, growth and reproduction should be positively selected. These predictions seem validated in our multi-species comparisons and the hypothesis of adaptive role in growth rate can be strengthened by the negative significant effect of environment on growth rate.

Maximal growth rate decrease when average temperature decreases and while this is not a novelty (e.g., Angilletta et al. 2004), the mirrored genetic-determined effect (positive) on growth rate point to a clear directional and adaptive selection for fast growth at high elevation. However, reasons of contradictory results of growth remain unsolved, but a possible explanation could lie in the measurement approach. In fact, growth is often measured between few and often temporally distant points. This approach can hide instantaneous event of fast growth (especially in alpine species which are regularly smaller), which can only be captured by frequent and repeated measurements under small temporal periods or by modelling growth trajectories.

Survival analyses support an environmental and genetic effect on species lifespan variation. Depending on how mortality of therophytes was treated (see material and method), effects of environment or origin of species may vary in its magnitude or sign. Species lifespan increases with increasing elevation both whether mortality was accounted for (reproductive) therophytes and if they were removed from the dataset. At first glance, this phenomenon could support reduced adaptation to cold environments, however it seems better explained by other reasons. For example, by delayed reproduction at high elevation, which postpone reproduction (and delay the associated mortality in therophytes), and by a biased dataset in favour of alpine species, which are more prone to survive under these conditions. More interesting is when the mortality of therophytes was accounted only if it is independent from reproduction. In this scenario, lifespan probability increases as the elevation increases suggesting that colder environments (upper-range) are not necessarily limiting species survival, which in contrast, can be less tolerant to low elevation conditions (e.g., warm or drier environments). However, the different responses across the three datasets suggests that ability to cope with climatic variations differs according to the life-history strategy, but our design does not allow an in-depth analysis of the phenomenon.

Whether climatic condition strongly differs across dataset, overall effects of origin was more consistent with a negative effect. Model suggests that with increase in elevation of origin, average

lifespan is reduced. Our results conflict with classical theory, which predict longer lifespan in alpine or arctic species, both at the levels of tissues (e.g., leaves) or individuals. However, Ehrlén and Lehtilä (2002) failed to find a significant variation in lifespan between plants from arctic/alpine to sub-tropical habitat indicating effects with other life-history traits (e.g., woody *vs* herbaceous or self-incompatibility). In a similar way, Körner (2003) reported that, once correctly accounted for season length, alpine species seem not differ from lower elevation plants species. A possible explanation of our results can be attributable to variation in shape of mortality. Although in no group (high or low elevation) there was a marked concentration of mortality in a specific time-point, the alpine ones showed higher mortality already in early life-stages following transplantation. Widespread mortality over time is likely to consequently explain the reduced life expectancy for alpine species as shown in our models. This phenomenon also seems to indicate that the early stages of recruitment are a particularly sensitive period in alpine species for which low seedling survival has been reported (Bliss 1971; Scherff et al. 1994; Forbis and Doak 2004). To conclude, we can say that variation in lifespan seems to be a distinctive characteristic between high- and low-elevation species, while species tolerance to climatic variation seems particularly good with overall survival probability of ~ 80% during the first year after germination.

Role of temperature for growth and survival

The temperature at which maximal growth – but not mortality – occurs enables the distinction from high- to low-elevation species. Specifically, alpine Brassicaceae can achieve faster growth under warmer climate. In line, others works reported positive association between warming environment and growth, e.g., Jarrad et al. (2009) has shown increased growth in several subalpine species subjected to warming and others demonstrated greater photosynthetic rate (Mächler and Nösberger 1977; Körner and Diemer 1987). Similar results have been found in a recent work, Maccagni and Willi (submitted) studied multi-traits selection within a phylogenetic framework under controlled

environment and reported faster growth in alpine species when subjected to warm spell (1 h at 41 °C). Results obtained under natural conditions thus confirm that alpine taxa can (or even are adapted to) exploit warm climatic windows, which can occur at higher elevation during sunny periods, to improve their growth. The evidence for preference of warmer climate suggests in a first-hand, that alpine species are not optimally adapted to cooler environment occurring at higher elevation, since under climatic adaptation we expected a shift in optima to colder temperature. In line, faster growth observed under warmer climate can be a consequence of counter gradient effect which has been reported from a variety of organisms (e.g., Hoffmann et al. 2005; Vitasse et al. 2009; Hodgson and Schwanz 2019), which emphasizes the basal adaptation (constitutive faster growth) when more suitable (i.e., warmer) conditions exist. On the contrary, the preference for cooler temperature in lowland taxa is in line with their winter-green strategy.

Surprisingly, no deadly temperature can be used to explain high or low elevation species. Species adapted to the upper- and lower-edges did not show a common response to the thermal components describing the elevational transect. This is line with previous findings of Maccagni and Willi (submitted), where authors reported no adaptive variation in thermal resistance in high *vs* low-elevation species. A first, simple explanation is that thermal resistance evolves to cope with microclimatic conditions resulting species-specific adaptation. Second, temperature could act indirectly, weakening the plants and making them less able to withstand further abiotic stress. Alternatively, mortality may depend on other factors. For example, dryness during summer periods or induced by frost (e.g., 2000 m resulted in the driest site during a snow-free time in December, based on volumetric soil moisture; data not shown) could significantly contribute to survival. Overall, divergent thermal-adaptation is unsupported and unlikely to explain observed upper or lower range-limits.

Adaptation to macro-climate in alpine species and variation in relative contribution of performance components

Our results indicate that species occurring along an elevational gradient are adapted to the prevailing climatic conditions of their elevation of origin. Signatures of adaptation at the level of *home* vs *away* was detected for lifetime performance and survival, but not for maximal growth rate despite it characterize high-elevation taxa. Refining the analysis in terms of *local* vs *foreign*, reproduction (as depicted by lifetime performance) becomes the trait which has the greatest influence on adaptation and, consequently, limits species distribution. Our results give partial support to studies on local – and climatic – adaptation, which reported constraint in reproduction at the lower edge and survival at the higher range in different plants species (e.g., in *Festuca eskia* (Gonzalo-Turpin and Hazard 2009); *Campanula thyrsoides* (Scheepens and Stöcklin 2013); *Erysimum capitatum* (Kim and Donohue 2013)); since we downgrade the role of survival, but we extend the role of reproductive constraints even at high elevation. More generally we indicate that reproductive failure is the main cause in explaining the restricted distribution of species in elevational gradients. Accounting for range-size variation does not improve the overall picture. Whether greater range size is hypothesized to be linked to a greater physiological flexibility, allowing the maintenance of high fitness over multiple environments (Brown 1984; Gaston and Blackburn 2008), its role in our work is limited. Wider range was able to ensure better survival, but its effect does not seem sufficient to buffer against the negative effects of the environment on reproduction. Consequently, greater physiological flexibility will allow establishment in environments outside the range, but long-term persistence is likely to be prevented by reproductive failure.

Reproduction is a key element, and our results indicate a link with growth and survival which varies according to environment and origin. Alpine species had lower contribution of lifetime performance, which however increases as elevation increase at the expense of reduced growth rate. Lowland plants had the opposite pattern: the difference between growth rate and reproduction is small

at low-elevation, but the gap increases as transplant-elevation increases. This indicates two things. First is that a trade-off between growth and reproductive performance seems to exist, i.e., alpine taxa have greater growth than they reproduction (in relative terms), and more generally, greater reproduction occurs at the expense of reduced growth. Second, the strength of this trade-off follows the environmental gradient as it increases as the difference in climate increases, suggesting a cost-allocation trade-off between performance components. Competition between reproduction and other function is not a novelty, and in plants negative correlation between reproduction and growth have been reported (e.g., Harper 1977). Specifically, to resource allocation, its variations have been already reported for alpine species, e.g., Douglas (1981) showed that allocation to vegetative, rather than to sexual reproduction decreased at the highest sites in *Mimmulus primuloides*. We can conclude that reduced reproduction is the main limitation in species expansion along an elevational gradient. This phenomenon seems to be strengthened by its competition with other performance-related traits, particularly growth, and which is aggravated by abiotic factors. However, further studies are needed to investigate whether and what is the specific role of temperature in this relationship.

CONCLUSION

Our study is among the first to investigate thermal adaptation in alpine plants species and the consequences for observed range limits within a phylogenetic framework involving 30 different species. Thermal adaptation is a wide recognised adaptation and constraint to range limits, however, although our results support climate adaptation with a decrease in lifetime performance with increasing distance from elevation of occurrence; we fail to find evidences for thermal adaptation. In fact, warmer conditions were optimal for growth rate in alpine species suggesting no thermal adaptation to colder, high-elevation environments and mortality was not linked to specific temperature. Our results indicate that alpine species have a shorter life span in the first year but are faster to grow. The relative relationship between growth and lifetime performance varies between

origin and environment and in particular lifetime performance increases at the proximity of the altitude of origin at the expense of growth. This suggests that a trade-off of resource allocation to reproduction may contribute to limit species' distribution along an elevational gradient.

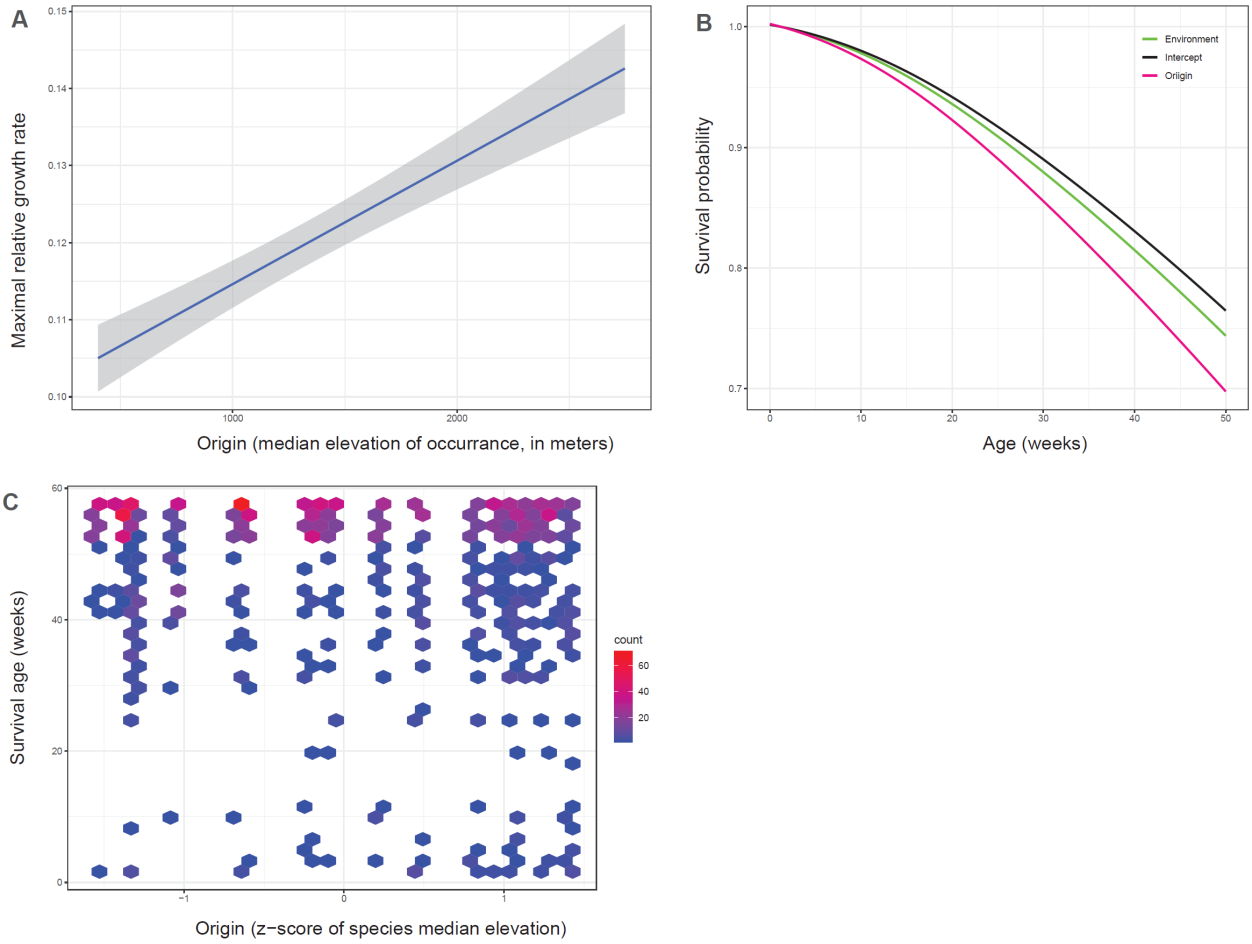

Figure 1 Variation in maximal growth rate and chance of survival along the elevational gradient accounting for origin. A. Relationship between maximal growth rate and elevation of transplant site for alpine (red) and lowland plants (blue). B. Weibull survival model showing chance of survival by time showing effect of environment (green), origin of plants (pink) and global intercept (black) and C. Pattern of survival along the time for each different origin (blue to red indicate variation in number of occurrence of mortality). Data comes from therophyte-altered dataset.

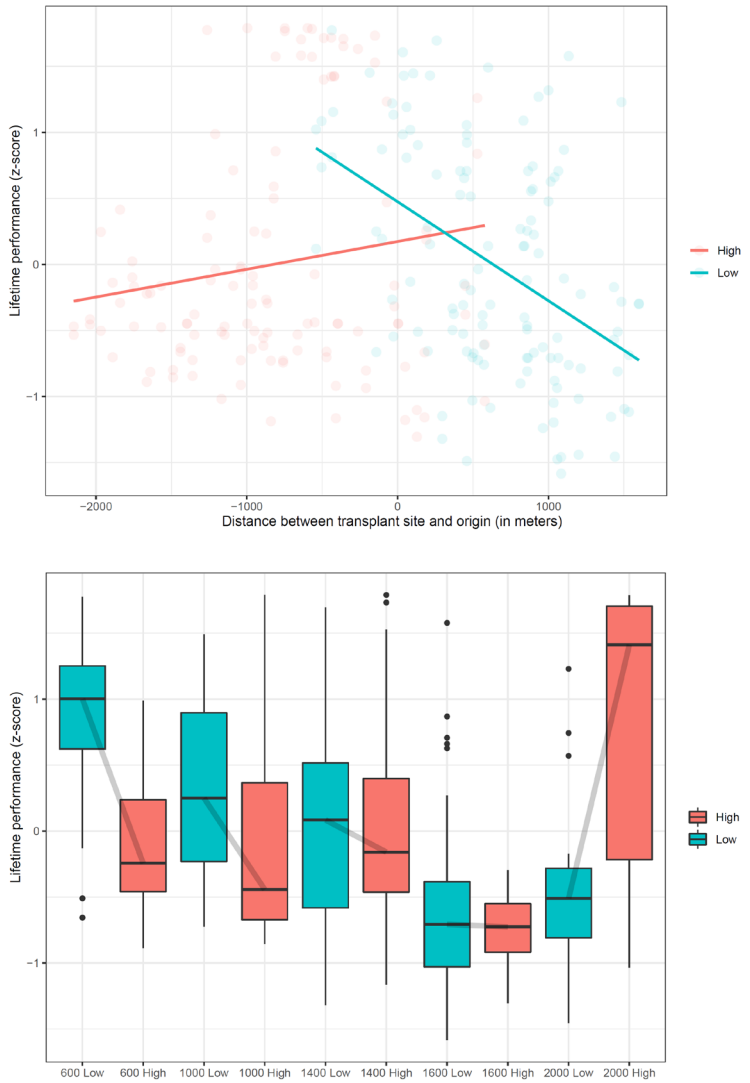

Figure 2 Variation in lifespan performance across the elevational gradient. *Top* Based on distance between the elevation of transplant site and median elevation of occurrence of the species, *Down* Based on comparisons between high and low elevation species within each site. A cut-off point at 1400 m asl is used to characterize high- (red) and low- (blue) elevation plants.

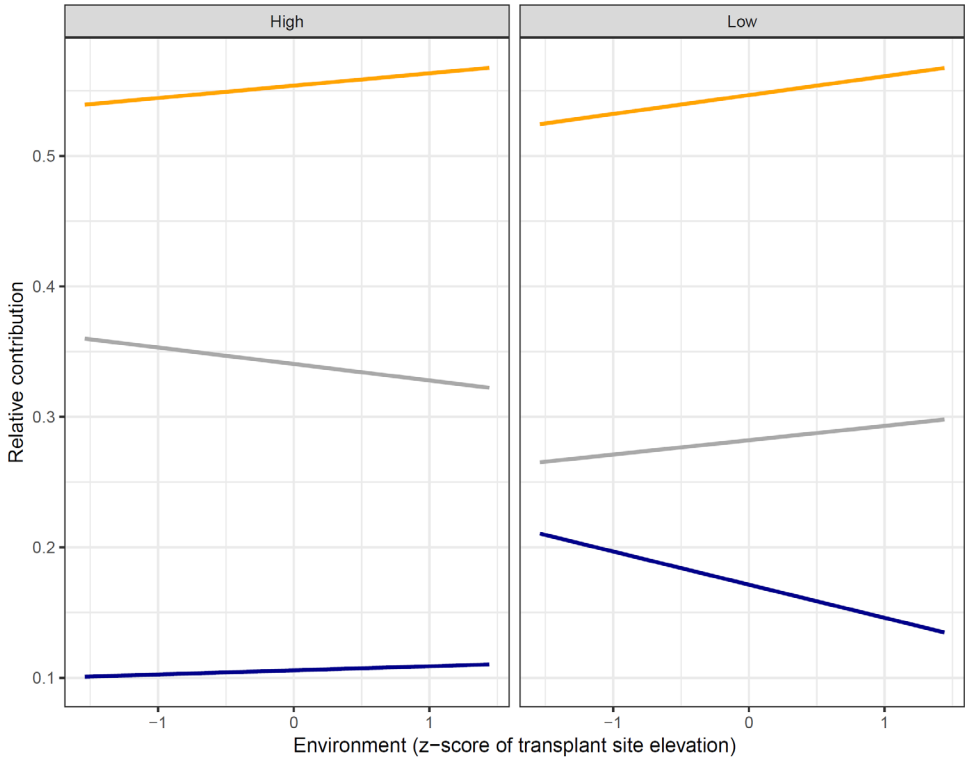

Figure 3 Variation in relative contribution of maximal growth rate (*grey*), lifespan performance (*blue*), survival (*orange*) accounting for origin of plants and elevation of transplant site (environment). High- and low- elevation were defined with a cut-off at 1400m asl.

Table 1 Location and thermal characterization of the transplant sites

							Temperature °C (+5cm)				
Site	**Elevation**	**Latitude**	**Longitude**	**Season**	**Start date**	**Days**	**Mean (±SD)**	**Mean min (±SD)**	**Abs. Min**	**Mean max (±SD)**	**Abs. Max**
Böfeli	601 m asl	46.87178	9.51882	Growing 2018	10 Oct.		8 ± 6	5 ± 4	-2	15 ± 8	27
				Winter 2018-19	12 Dec.	41	0 ± 3	-3 ± 6	-4	6 ± 2	7
				Growing 2019	22 Jan.		13 ± 8	7 ± 1	-1	21 ± 9	42
				Winter 2019-20	12 Dec.	112	8 ± 9	1 ± 3	-1	20 ± 9	29
				Overall			**11.0 ± 8.5**	**6.0 ± 5.9**	**-4**	**19.3 ± 9.3**	**42**
Arella	997 m asl	46.8738	9.50872	Growing 2018	26 Sept.		9 ± 7	5 ± 5	-3	16 ± 10	28
				Winter 2018-19	13 Dec.	96	0 ± 1	-1 ± 1	-3	2 ± 3	7
				Growing 2019	19 Mar.		12 ± 9	7 ± 6	-2	21 ± 10	41
				Winter 2019-20	12 Dec.	112	7 ± 9	0 ± 2	-1	21 ± 9	29
				Overall			**9.7 ± 8.8**	**4.8 ± 5.6**	**-3**	**17.8 ± 11.1**	**41**
Nesslaboda	1'395 m asl	46.86922	9.49018	Growing 2018	20 Sept.		11 ± 6	6 ± 2	2	20 ± 6	30
				Winter 2018-19	16 Nov.	170	1 ± 4	0 ± 3	-7	3 ± 6	22
				Growing 2019	05 May		11 ± 9	6 ± 5	-4	20 ± 11	40
				Winter 2019-20	12 Dec.	111	5 ± 8	-1 ± 2	-2	14 ± 12	26
				Overall			**7.8 ± 8.6**	**3.7 ± 5.1**	**-7**	**14.3 ± 11.8**	**40**
Fontanulliaris	1'610 m asl	46.87768	9.49451	Growing 2018	12 Sept		7 ± 7	3 ± 5	-7	14 ± 10	27
				Winter 2018-19	24 Dec.	132	1 ± 3	0 ± 1	0	2 ± 6	20
				Growing 2019	05 May		10 ± 8	6 ± 5	-2	19 ± 11	38
				Winter 2019-20	12 Dec.	112	5 ± 8	-1 ± 1	-2	15 ± 11	25
				Overall			**7.2 ± 8.2**	**3.4 ± 4.7**	**-7**	**13.7 ± 11.6**	**38**
Neusäss	1'998 m asl	46.88786	9.48949	Growing 2018	14 Aug		11 ± 7	4 ± 2	0	21 ± 5	28
				Winter 2018-19	27 Oct	192	0 ± 3	-1 ± 3	-12	1 ± 3	10
				Growing 2019	07 May		9 ± 8	4 ± 3	-3	18 ± 10	35
				Winter 2019-20	11 Nov.	159	1 ± 5	-2 ± 2	-6	5 ± 8	18
				Overall			**5.4 ± 7.7**	**1.5 ± 3.9**	**-12**	**11.1 ± 11.0**	**35**

Table 2: Mixed-effects model testing for effect of environment, origin and range size on growth and survival. Origin is the median elevation of occourence of each species, environment is the elevation of the common garden. Maximal growth rate is the maximal increase in number of leaves during the first year after transplanting. Survival reflect the probability of survival during the first year (time in weeks).

	Intercept	Environment	Origin	Range size
Maximal relative growth rate	**-0.193**	**-0.068**	**0.089**	0.030
HDI 90%CI	**[-0.279, -0.115]**	**[-0.083, -0.054]**	**[0.058, 0.119]**	[-0.001, 0.060]
pd	0.999	1	1	0.947
Survival (weeks, Weibull)				
Complete	**4.215**	**0.104**	-0.039	0.150
HDI 90%CI	**[3.589, 4.836]**	**[0.080, 0.126]**	[-0.212, 0.141]	[-0.011, 0.322]
pd	1	1	0.644	0.926
Modified terophyte	**4.616**	**-0.056**	**-0.183**	0.151
HDI 90%CI	**[4.088, 5.165]**	**[-0.091, -0.020]**	**[-0.350, -0.019]**	[-0.016, 0.303]
pd	1	0.994	0.965	0.934
Removed terophyte	**4.705**	**0.115**	**-0.377**	0.056
HDI 90%CI	**[4.088, 5.257]**	**[0.071, 0.156]**	**[-0.610, -0.163]**	[-0.162, 0.268]
pd	1	1	0.996	0.668

Bold highlight values differents from zero within the high-density interval of the 90% credible interval

Table 3: Logistic mixed-effects model testing for effect of thermal descriptors linked to maximal growth rate and mortality and probability of belong to high or low elevation class. Predictors variables were centred and scaled. Crossed random effect were species and block.

Origin (High:1, Low:0)	Intercept	Mad	Max	Min	Cumulative heat	Cumulative frost	Days of frost
Maximal growth rate	-0.514	-0.658	**4.116**	-0.539	2.877	-0.143	-
HDI 90%CI	[-4.142, 3.269]	[-2.984, 1.831]	**[0.247, 9.063]**	[-2.974, 2.249]	[-0.763, 7.429]	[-2.596, 2.350]	-
	0.597	0.678	0.97	0.643	0.906	0.542	
Mortality	-0.075	0.092	-0.467	1.155	0.006	-	-0.988
HDI 90%CI	[-4.846, 5.129]	[-2.661, 2.947]	[-3.955, 3.317]	[-2.441, 5.541]	[-3.488, 3.685]	-	[-4.318, 2.221]
	0.5129	0.525	0.585	0.694	0.501		0.692

Bold highlight values different from zero within the high-density interval of the 90% credible interval

Table 4.1: Mixed-effects model testing for *home-way* effect. Distance between common garden and origin (Δ-Elevation), on performance estimates was tested. Predictors variables were centred and scaled, and performance estimates were centred and scaled across site independently for each species-block. Crossed random effect were species and block.

	Intercept	**Origin × Δ-Elevation**	**Origin × Δ-Elevation²**
Maximal growth rate	0.019	0.029	0.035
HDI 90%CI	[-0.576, 0.636]	[-0.120, 0.159]	[-0.025, 0.096]
	0.537	0.64	0.818
Survival ratio	0.157	**0.222**	**0.097**
HDI 90%CI	[-0.420, 0.690]	**[0.089, 0.349]**	**[0.040, 0.153]**
		0.997	0.997
Lifetime performance	0.256	**0.359**	**0.082**
HDI 90%CI	[-0.348, 0.833]	**[0.209, 0.501]**	**[0.020, 0.147]**
		99.98	98.33

Table 4.2: Mixed-effects model testing for *home-away* effect. Distance between common garden and origin (Δ-Elevation) and range-size, on performance estimates was tested. Predictors variables were centred and scaled, and performance estimates were centred and scaled across site independently for each species-block. Crossed random effect were species and block.

	Intercept	**|Δ-Elevation|**	**|Δ-Elevation| × Range size**
Maximal growth rate	0.01	-0.025	0.020
HDI 90%CI	[-0.566, 0.548]	[-0.130, 0.074]	[-0.089, 0.129]
	0.523	0.654	0.615
Survival ratio	0.036	**-0.106**	**0.229**
HDI 90%CI	[-0.533, 0.520]	**[-0.192, -0.021]**	**[0.138, 0.318]**
	0.601	0.977	1
Lifetime performance	0.009	**-0.264**	0.084
HDI 90%CI	[-0.548, 0.496]	**[-0.353, -0.174]**	[-0.012, 0.180]
		100	91.8

Bold highlight values differents from zero within the high-density interval of the 90% credible interval

Table 4.3: Mixed-effects model testing for *local-foreign* effect. Effect of origin within common garden on performance estimate was tested. Origin was centred and scaled to unit variance, and performance estimates were centred and scaled across site independently for each species-block. Crossed random effect were species and block.

	Origin × 600	**Origin × 1000**	**Origin × 1400**	**Origin × 1600**	**Origin × 2000**
Maximal growth rate	-0.07	**0.206**	-0.147	0.108	-0.094
HDI 90%CI	[-0.258, 0.104]	**[0.019, 0.392]**	[-0.348, 0.050]	[-0.088, 0.303]	[-0.290, 0.105]
	0.733	0.96	0.882	0.81	0.787
Survival ratio	-0.145	0.034	0.066	**-0.391**	**0.425**
HDI 90%CI	[-0.323, 0.046]	[-0.146, 0.225]	[-0.125, 0.244]	**[-0.578, -0.205]**	**[0.235, 0.606]**
	0.892	0.609	0.711	1	0.999
Lifetime performance	**-0.354**	**-0.244**	-0.099	-0.124	**0.837**
HDI 90%CI	**[-0.528, -0.167]**	**[-0.426, -0.070]**	[-0.276, 0.074]	[-0.300, 0.054]	**[0.662, 1.028]**
	0.998	0.984	0.822	0.874	1

Bold highlight values differents from zero within the high-density interval of the 90% credible interval

Table 4.4: Mixed-effects model testing for *local-foreign* effect. Effect of range-size and distance within common garden on performance estimate was tested. |Δ-Elevation| and range size were centred and scaled to unit variance, and performance estimates were centred and scaled across site independently for each species-block. Crossed random effect were species and block.

	|Δ-Elevation| × Range size × 600	**|Δ-Elevation| × Range size × 1000**	**|Δ-Elevation| × Range size × 1400**	**|Δ-Elevation| × Range size × 1600**	**|Δ-Elevation| × Range size × 2000**
Maximal growth rate	0.005	-0.092	-0.015	0.191	0.022
HDI 90%CI	[-0.145, 0.156]	[-0.322, 0.167]	[-0.339, 0.265]	[-0.063, 0.443]	[-0.160, 0.196]
	0.522	0.718	0.537	0.884	0.579
Survival ratio	**0.324**	-0.029	0.044	**0.243**	**0.332**
HDI 90%CI	**[0.178, 0.480]**	[-0.252, 0.190]	[-0.240, 0.332]	**[0.008, 0.475]**	**[0.162, 0.506]**
	1	0.584	0.605	0.946	0.999
Lifetime performance	0.129	-0.054	0.040	**0.283**	-0.043
HDI 90%CI	[-0.033, 0.301]	[-0.291, 0.179]	[-0.264, 0.347]	**[0.059, 0.527]**	[-0.233, 0.169]
	0.891	0.641	0.582	0.973	0.628

Bold highlight values differents from zero within the high-density interval of the 90% credible interval

Table 5: Mixed-effects model testing for effect of origin and environment on variation in relative contribution of performance components (maximal growth rate, survival fraction and lifetime performance). Predictors variables were centred and scaled. Crossed random effect were species and block Maximal growth rate is used as contrast.

		Median (posterior)	HDI 90%CI	
Survival	Intercept	0.576	[-0.284, 1.405]	0.918
	Environment	**0.039**	**[0.009, 0.072]**	0.974
	Origin	**-0.180**	**[-0.250, -0.114]**	1.000
	Environment^2	**0.057**	**[0.022, 0.089]**	0.997
	Origin^2	-0.059	[-0.144, 0.032]	0.855
	Origin × environment	0.018	[-0.014, 0.049]	0.820
Lifetime performance	Intercept	-0.972	[-1.884, 0.208]	0.930
	Environment	**-0.047**	**[-0.094, -0.003]**	0.948
	Origin	**-0.252**	**[-0.367, -0.125]**	0.999
	Environment^2	**0.095**	**[0.049, 0.145]**	0.999
	Origin^2	0.018	[-0.150, 0.170]	0.574
	Origin × environment	**0.116**	**[0.071, 0.160]**	100.00

Bold highlight values different from zero within the high-density interval of the 90% credible interval

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CHAPTER 4

Divergence in phenology and reproduction in Brassicaceae species differing in elevational distribution

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Acknowledgements

We thank Lea Bona, Camilla Jenny, Adrian Möhl, Ramon Müller, Jens Paulsen, Florian Schreier, and Daniel Slodowicz, for collecting seeds in the field. Georg Ambruster, Jens Paulsen, Marco Barandun and Fabian Heussler helped with the setting up of the field sites. Georg Armbruster, Olivier Bachmann, Markus Funk, Michela Meier, Susanna Riedl, helped with setting the field-site, sowing seeds, and fruitful discussions. Amos a Marca, Maya Bosshard, Nicolas Feigenwinter, Adrian Metry, Bianca Modespacher, Laura Rieder, Magdalena Samland and Basil Willi for helping taking plant measures. The ETH Zürich (Institute of Integrative Biology) and the municipality of Haldenstein provided access to field sites. Finally, we would like to thank all the field botanists that contributed with occurrence data to the InfoFlora database.

ABSTRACT

Living organisms typically occur over restricted space where they can maintain viable populations. A decline in reproductive output from the centre to the periphery of the range indicates environmental or genetic limitations in growth, survival and reproduction, which can provide an ecological explanation for range limits. In the current work, we investigated the extent to which reproduction is affected by the environment across an elevational gradient, and how this differs among species with different elevational ranges. We performed a transplant experiment on 30 Brassicaceae species with colline to alpine distributions. Plants were raised in five common gardens along an elevational transect, from 600m to 2000m, in the central Alps. We assessed survival, size at reproduction, the initiation of flowering, and the time needed for fruit ripening. Data were used to test for variation in aspects of performance due to garden and species' elevational distribution, for phenological plasticity, and for costs of reproduction. Results indicated that the probability of reproduction declined with elevation and origin, but species had highest fruit production at an elevation typical for their distriubtion. Time for ripening was not different among species and elevational sites, and the transition to flowering was affected only by site but did not differ among the elevation of species occurrence. Reproduction reduced the chance of subsequent overwinter survival independently from size variation, but alpine species were less affected. However, bigger flowering plants resulted in higher fruits number in lowland plants, but not in alpine species. Our results indicate that species are limited at their upper- and lower- elevational range-limits by interplay involving reproduction, growth and survival.

Key words: Phenological plasticity – Phylogeny – Range-Limits – Reproductive ratio – Reproductive costs – Reproductive size

INTRODUCTION

Living organisms exist in restricted geographical space and their occurrence is largely determined by their ability to maintain viable population under varying environmental conditions. In fact, is often assumed that the geography of species is linked with their niche (Hargreaves et al. 2014; Lee-Yaw et al. 2016), such that species reach a limit of tolerance under boundary conditions and are maladapted to those beyond the range (Antonovics 1976). Consequently, populations are exposed to unfavourable conditions at and beyond range edges, which affects physiology, growth, survival and reproduction. In agreement with that, individual performance has been found to decline near and beyond the edge where survival and fecundity decrease (e.g., Pigott and Huntley 1981; Caughley et al. 1988; Sagarin and Gaines 2002; Jump and Woodward 2003; Angert and Schemske 2005). More generally, stressful environments, which occurs at range margins, will translate into reduced individual and mean performance at the edge, and may lead to demographic sinks (Hargreaves et al. 2013). In this article, we examine whether constraints in reproduction can explain observed range limits along a short thermal gradient, over elevation.

Survival and reproduction are critical in the maintenance of populations of species since they affect their population growth rate and ultimately long-term persistence in a given habitat. Like most developmental processes, they are extremely sensitive to external factors, such as climatic conditions or biotic interactions (e.g., pollinator availability in plants). For example, increased temperature can boost the rate of flowering and fruit production (Ainsworth and Ort 2010), but can become unfavourable inducing floral sterility (Morrison and Stewart 2002) or decreasing survival (Prasch and Sonnewald, 2015). The thermal environment can also have long-terms influence on performance, e.g., by determining speed of fruit production after flowering occurs and consequently defining the available time for reproduction. In seasonal climates (e.g., higher elevation), timing of reproduction is crucial, since premature or late reproduction can expose living organisms to unsuitable conditions, leading to reproductive failure (Inouye 2008)).

Along an elevational gradient, plant species show great variability in their phenological and reproductive response, often with contrasting patterns. For example, some studies have found genetic fixation as an evolutionary consequence to avoid frost damage (Keller and Körner 2003). Similarly, in some species higher reproductive success comes from earlier flowering time (Giménez-Benavides et al. 2007), while in others later reproduction seem most advantageous (Inouye 2008). Timing of seasonal activities has thus evolved to be triggered by consistent environmental factors, to guarantee reproductive success (Rathcke and Lacey 1985) within specific environmental factor, but potentially becoming maladaptive in different environments resulting in reduction in fecundity. However, phenological plasticity seems another powerful way to guarantee reproduction, since it allows organisms to be exposed only within a favourable climatic window, no matter when it occurs, inside the full climatic conditions of a given location (Donohue 2002). Consequently, phenological plasticity can influence the probability of fruit maturation (e.g., Pigott and Huntley 1981; Kozłowski 1992; Galloway 2002) and reproductive success (e.g., Giménez-Benavides et al. 2007; Inouye 2008). A good example demonstrating the role of reproductive plasticity was show by Griffith and Watson (2006), where induction of earlier reproduction of *Xanthium strumarium* enabled production of mature seeds beyond its northern range of occurrence in North America. Also other studies supported environment-induced effects such as earlier flowering under warmer conditions (Scheepens and Stöcklin 2013; Frei et al. 2014).

While reproduction may be guaranteed either by fixed programs or plastic responses, it seems to reach limits at range edges. Evidence for reduced reproductive output come from the observations of faster reproduction close to northern edge. Some authors observed that, at northern edges of distribution, sexual maturity was anticipated with individuals being reproductive at younger age or at smaller size (e.g., Amundsen et al. 2012; Colautti and Barrett 2013; Dangremond and Feller 2016). Reproductive size is known to positively affect reproduction and offspring quality both in animals (e.g., Stearns 1992) and plants (Sletvold 2002; Montague et al. 2008), possibly due by better access

to resources. In monocarpic species, larger individuals resulted in increased female function and reproductive output (de Jong et al. 1989). Consequently, variation in size close to the edge can explain the observed depressed reproduction indicating potential sex-growth allocation trade-offs. Unfortunately, they have been rarely studied across gradients (e.g., Griffith and Watson 2005) resulting in a still unexplored role of this trade-offs in geographic limit.

Here we explored the extent to which such differences in the timing of reproduction and other aspects of the life history can contribute to shaping the elevational distribution in plant species in a macroevolutionary framework. Our study involved 30 Brassicaceae species occurring in the central Alps of Europe, with a median elevation ranging from 400 to 2750 m a.s.l. This system has already provided support for divergent adaptation along the elevational gradient, while the limiting environmental factors differ at the low and high end of their distribution (Maccagni and Willi 2020; Chapter 3; Patsiou et al. 2020). In particular, it was found that high-elevation species have a faster growth under warm conditions, and that the propensity to speed up growth and possibly development sets the upper elevation range limit. Here we explored whether also the shift to sexual reproduction was earlier and associated with the upper range limit. Furthermore, we studied in more depth low-elevation range limits. From fall 2018 to spring 2020, plants of 30 species were grown in common gardens at 5 sites along an elevational gradient (from 600 to 2000m a.sl), arranged along a 3-km transect in the central Alps. We recorded the phenology of sexual reproduction (i.e. time to flowering and time to ripe fruits), plant size at reproduction, fruit production and over-winter survival. We investigated the following questions: i) To what extent is reproductive performance affected by the environment and the elevation of origin of plant species? ii) Is there variation in reproductive time and time of flowering-onset along the gradient? and what is the contribution of the origin of the species? And iii) Are there costs associated with reproduction, and how do those differ among species and among transplant sites depending on whether they are within or outside the range of natural occurrence of a species?

MATERIAL AND METHODS

Choice of species and sampling

Thirty species belonging to the Brassicaceae family and naturally occurring in the central European Alps, from the colline to the alpine life zone,were selected. They were part of two species-rich tribes occurring in the Alps (Cardaminae and Arabideae) and had similar ecological requirements (i.e. Landolt's moisture indicator values between 2 and 4), but they differed in elevational distribution. The species list is available in supplementary material A1. Seeds were collected from March to September during the years 2015-2017 at two different sites in the Swiss Alps located at least 50km apart from each other, and preferentially from different biogeographic regions. The sites were at the most common elevation for each species. Seeds sampled from separate plants in the field were stored separately in paper bags (80 g m^{-2}, 60 × 90 / 12 mm, ELCO AG, Brugg, Switzerland) under cold (4 °C), dark and dry (added silica gel) conditions until sowing.

Sowing, pre-growth conditions and transplant site

Design – The experimental design involved the raising of 30 species, each represented by 2 populations and 5 plants from which seeds were collected per population in the field, i.e. 10 seed families per species. The experiment was split into 5 transplant sites at different elevations, with two blocks/replicates per site, and each block containing the 10 seed families per species. The final design resulted in 600 individuals *per* site and 3'000 in total (30 species × 10 seed families × 2 blocks/replicates × 5 sites = 3'000 individuals). The sowing was done in 5 rounds, one for each transplant site, such that when seedlings were brought out to a transplant site in late summer to fall, average temperature conditions were comparable.

Sowing and pre-growth conditions – Seeds of each seed family were haphazardly selected. Seeds were incubated in 500µl of gibberellic acid solution (500ppm, Merck KGeA, Dornstadt, Germany) for 1 week in dark and cold (4°C constant; Climecab 1400 Kälte 3000 AG, Landquart,

Switzerland) to trigger synchronous germination. Then seeds were sown by random spatial order in multipot-trays (0.2L, 28 pots per tray 6×7cm, Quick-Pot QP; gvz-rossat.ch, Otelfingen, Switzerland), filled with a mix of soil (bark compost, peat and perlite; Aussaat- und Pikiererde; Oekohum, oekohum.ch, Herrenhof, Switzerland) and sand (0-4mm) in a ratio of 2:1; and transferred in growth chambers (MobyLux GroBanks, CLF Plant Climatics, plantclimatics.de, Wertingen, Deutschland). All growth chambers were located inside a PlantMaster (CLF, Plant Climatics, plantclimatics.de, Wertingen, Deutschland) with controlled humidity and temperature. Trays were kept at 15/18 °C night:day, 75% relative humidity (RH), light:dark 8:16 h at 200 μmol m^2 s^{-1} (fluorescent white lamps and red-LED). After 3 weeks, excess seedlings were used to fill pots without any germination. In week 4, light was gradually increased to maximal capacity (400 μmol m^2 s^{-1}, by steps of 50 μmol m^2 s^{-1} every second day) to acclimate plants to field conditions. Plants where moved to the transplant sites at 2- to 4-leaf stage.

Transplant sites – Five different sites (Tab. 1), representing different elevational life-zones, were selected along a 3-km transect on a south-facing slope in Calanda region (Switzerland; Lat. 46.875, Long. 9.501), in the central Alps: colline ("Im Bofel", 600 m a.s.l.), montane ("Arella", 1'000 m a.s.l.), mid-montane ("Nesselboden", 1400 m a.s.l.), alti-montane ("Oberberg", 1'600 m a.s.l.) and subalpine ("Gruoben", 2'000 m a.s.l.). Multipot-trays with germinated plants were moved to the field sites in fall, when predicted daily mean temperature based on the nearest meteo-station were dropping to around 10 °C, starting with the site on the top and ending on the bottom (14/08/2018, 12/09/2018, 20/09/2018, 26/09/2018, 10/10/2018). The trays were buried into soil and arranged in two spatially separated blocks, each composed of 11 trays arranged in 2 parallel rows. During the first week, trays were covered by a shading net and watered twice a week with 20 L of water per block. Then the netting was removed and watering reduced but maintained during part of the first fall to compensate for the reduced substrate volume in the pots and high evaporation when needed. At each site, temperature was recorded 5 cm above the soil surface ("micro-climatic" temperature) every 15 min

(Thermologger, TOMST s.r.o., Prague, Czech Republic) by 4 loggers installed above randomly selected empty pots and spit across the two blocks.

Trait assessment

Phenology monitoring – From 2018 to the end 2019, plants were checked weekly for flowering and fruiting. Two main transitions were recorded: onset of flowering and of ripe fruits. Flowering onset was defined as first, fully opened flower. Onset of ripe fruits was the time when the first opened/ripe silique was observed. The date on which each of the two transitions were observed was recorded (in days of the year) and used to describe the date of flowering (DF) and the date of fruiting (DR) respectively. Time to ripe fruits was derived as the number of days between DR minus the DF (RT, for ripening time).

Performance – Size at reproduction was recorded as the mean length of the two longest leaves (healthy and green), both during onset of flowering and ripe fruits. As an additional measure, the final height was measured at the date of onset of ripe fruits and describe the height from the ground to the highest point (i.e. the top of the inflorescence). Reproductive output (REPO) was used as proxy of performance. It was calculated by the number of fruits (i.e. siliques) produced at the time when the first ripe fruit was scored. Inflorescences were collected in paper bags, dried at 65 °C for 48 h for storage, and subsequently fruits counted. For big inflorescences (> 50 fruits *per stem*) with homogenous fruits sets, fruits production was estimated by counting number of fruits along a 5 cm fragment, then multiplied for the stem length; if multiple stems where produced, the same procedure was independently applied to each of them and final values summed. Finally, in perennial plants species, overwinter survival (OWS) was added as an additional performance component. Survival was recorded as binary outcome (alive/death) in spring 2019 and 2020. Mortality was assigned when plants were completely dry, with no more green tissue neither in apical or lateral buds and winter-

time starting after 5 consecutive days with mean temperature ≤ 0 °C, and ending after 5 consecutive days with a mean temperature > 0 °C.

Statistical analysis

Influence of origin and environment on reproduction – The effect of elevation of transplant site (environment; continuous variable), median elevation of occurrence of species distribution (origin; continuous variable) and their interaction on occurrence of flowering and fruit ripening were tested using a logistic-regression generalised linear mixed models based on Markov Chain Monte Carlo techniques with the 'brm' function of the package {brms} (Bürkner 2017). The response variable was modelled by a Bernoulli family distribution and it represent the state of the trait at the end of the season (1 if the individual flowered/produced fruits). Model were constructed with a crossed random effect, with varying intercept, composed by a nested design accounting for species (maternal-line within population, population within species) and block/replicate effect.

The effect of environment, origin of species and their interactions on reproductive output were tested with a Bayesian mixed-effects model. Values were pooled at species level independently for each block within site. Block and species relatedness were used as crossed random effect modelling a varying intercept.

All analyses and figures were performed using the statistics software R v. 4.0.2 (R Core Team 2014). Data manipulation was performed with the {tidyverse} suite and time operation with the {lubridate} package (Spinu et al. 2018). Where not differently specified, mixed-effects models were performed with Student's t distribution to improve robustness (i.e. reduces sensitivity to outliers) and species relatedness was accounted by a variance-covariance matrix. Information on species relatedness came from a phylogeny produced based on several dozen chloroplast genes (Patsiou et al. 2020) and was pruned to species included in this study with the unction 'treedata' of package geiger (Harmon et al. 2008). The final matrix was obtained with function 'vcv' {ape} (Paradis and Schliep

2018) and specified within the 'cov_ranef' setting in 'brm'. All the predictors and continuous response variables were centred to mean 0 and scaled to unit variance to improve model convergence, and median elevation of origin previously log_{10}-transformed to improve normality. Posteriors were reported as median values, and significance evaluated as 90% credible-interval (CI90) of the high density interval and decisions based on probability of direction with the {bayestestR} package (Makowski et al. 2019). Values were drawn from four independent parallel chains, where burn-in, number of iterations and thinning interval, as well as maximal tree-depth and adaptive delta were adjusted for each model to have an effective sampling size (ESS) of at least 1000. Model convergence was checked by visually inspecting diagnostic plots and Rhat statistic values. Calculations were performed at sciCORE (http://scicore.unibas.ch/) scientific computing centre at University of Basel.

Plasticity in reproductive phenology – The effect of environment, origin and their interaction (i.e. phenological plasticity) on flowering date were tested using a Bayesian mixed-effects model. The response variable was the date of flowering (DF, as day of the year), averaged at maternal-line level across blocks within site. Random intercept and slope were modelled by maternal-line within population, within species. An analogue model was performed using the number of days following winter end (i.e., date of flowering - date when winter ends) as response variable.

A second set of models was performed to test the effect of environment, origin and their interaction on ripening time (RT). The response variable was RT, averaged at maternal-line level across blocks within site and log_{10}-transformed to improve normality. Random intercept and slope were modelled by maternal-line within population, within species. An analogue model was built to test change in variance of RT. Response variable was the coefficient of variation of RT, calculated at the species level within site, as the standard deviation divided by the mean of RT. Random intercept and slope were modelled by species relatedness.

Cost of reproduction – Two set of models were performed to test whether reproduction affect survival and whether increased elevation impose faster sexual maturity at expense of smaller size. For the first case, a first model predicted over-winter mortality based on flowering (1/0, categorical), fruit ripening (1/0, categorical), origin and their interactions; while a second model tested for size at reproduction, origin and they interactions on the same response variable. Sizes were log_{10}-transformed (+1). Random slope and intercept were maternal-line within population, nested within species and crossed effect were block/replicate. Bernoulli family distribution was used to predict over-winter mortality.

The second case, size at flowering, fruiting and height were modelled as response variables and origin, environment and interaction used as predictor variables. Size values were log_{10}-transformed (+1) to improve normality. Analysis were performed on averaged maternal-line values across blocks within sites and predictors and response variables mean centred and scaled to unit variance to improve model convergence. Random effects were maternal-line within population, nested within species.

A final model was performed to test whether bigger size promote higher reproductive output. Specifically, response variable was mean reproductive output (log_{10} + 1) for each species within each block-site, and predictors variables were the additive effect of rosette size at flowering and at reproducing time *per sè* and in interaction with species origin. Species relatedness and block modelled a random intercept.

RESULTS

Influence of environment and origin on reproductive performance

Results of Bayesian mixed-effects model for effect of the elevation of the transplant site (environment) and the elevation of origin of species (origin) on reproduction are summarised in Tab. 2, Fig. 1. The environment and origin were negatively associated with the propensity to flower (-0.442, CI90%[-0.794, -0.064]; -0.626, CI90%[-0.731, -0.524]), on the contrary the effect of the

interaction had a certainly existing probability of being positive (0.721, CI90%[0.623, 0.828]). In line were the results for the propensity to bear ripe fruits (Tab. 2); i.e., high-elevation (both as environment and origin) reduced the propensity to reproduce, which was greater for plants grown in climatic environments closer to their natural distribution.

Mean reproductive output in response to experimental transplantation was unaffected both by environment and origin (Tab. 2). However, the effect of the interaction between environment and origin was likely to be positive with a probability of 96% (1.532, CI90%[0.062, 2.889]), i.e., there was no difference in the reproductive output between high- and low-elevation species, but plants produced larger fruits number at the site reflecting climatic conditions closer to the environment where these plants were expected to be.

Phenological plasticity

Results of Bayesian mixed-effects model testing for genetic (elevation of origin of species), environment (elevation of the transplant site) and plastic response (i.e., interaction) on flowering date, are summarised in Tab. 3.1, Fig. 2. The effect of the environment had a probability of 100% of being positive (0.772, CI90%[0.652, 0.901]), while the genetic and the plastic effect had a respective probability of 58% and 84% of being negative (-0.028, CI90%[-0.312, 0.219]; -0.055, CI90%[-0.153, 0.048]). The use of the number of days following the end of winter, instead of the flowering date, shows similar results (Tab. 3.1). Ripening time (RT, i.e. time from flower onset to first ripe fruit) was unaffected by origin, environment, or their interaction (Tab. 3.2, Fig. 2). What we have learned is that high- and low-elevation species did not differ either in flowering date, which depends solely on environmental factors, or in ripening time.

Cost of reproduction

The effect of origin of plants, environment and their interaction on performance depicted by size at reproduction, are reported in Tab. 4, Fig. 3. The size at the time of flowering onset was negatively related to origin (-0.386, CI90%[-0.733, -0.019]) and environment (-0.176, CI90%[-0.323, -0.041]), but not by the interaction, which resulted in a positive trend (0.074, CI90%[-0.007, 0.154]). The size at the time of the onset of the first fruits was related only to the elevation of the transplant site (i.e., environment) with a likely existing negative effect (-0.099, CI90%[-0.209, -0.011]), i.e., alpine species flowered at smaller size and climatic conditions at high elevation was reflected in reduced reproductive size. Plants height was affected by origin, which resulted in a possibility existing effect with a probability of 95% of being negative (-0.649, CI90%[-1.225, -0.031]), while the interaction between origin and environment, had a 97% probability of being positive resulting in likely existing effect (0.062, CI90% [0.004, 0.112]). To summarise, alpine species were constitutively shorter but reproductive height increased at higher elevation.

Over-winter survival was not related origin and size at reproduction (Tab. 5, Fig. 3). On the other hand, the propensity to survive the winter-period depended on the occurrence of reproduction, with the effect of successful flowering and fruiting having a 97% and 96% probability of being positive respectively (0.860, CI90%[0.120, 1.560]; 0.628, CI90%[0.05, 1.190]). The effect was reversed interaction between origin and fructification was taken into account, which resulted in a 95% probability of being negative (-0.616, CI90%[-1.216, -0.036]). We conclude that reproducing during the year reduced the probability of surviving the winter, but that alpine species can tolerate it better.

Although the size at the time of the onset of flowering (or fruits) did not affected over-winter survival, the same was not true for reproductive output (Tab. 6, Fig. 3). The mean fruit production varied positively with plant size at flowering and fruiting time (0.365, CI90%[0.257, 0.468]; 0.112, CI90%[0.027, 0.203]). Adding the interaction between reproductive size and origin, revealed a likely existing effect of size during flowering onset and origin, with a 98% of probability of being negative

(-0.149, CI90%[-0.260, -0.045]). As a result, larger plants produced more fruits, but alpine species were more productive by flowering at smaller sizes.

DISCUSSION

Possible ecological explanation of the range limits can be attributed to reduced reproductive performance observed close to the edge of distribution; but open questions remain, e.g., how does reproduction differ between species adapted to the upper and lower edge? Our results indicate declining reproductive performance in 30 Brassicaceae species of central Alps, when they approach the edge of their distribution along an elevational gradient. In general, alpine species differs from lowland plants by having a greater propensity to reproduce (and producing more fruits) at high elevation, reproducing at smaller sizes and being more likely to over-winter survival despite reproducing. Results are discussed regarding reproductive adaptation and the consequences for elevational range-limits.

Influence of environment and origin on reproductive performance

Species have a greater propensity to reproduce (and produce more fruits) the closer they are to the environmental conditions where they are expected to be. This is in line with a number of studies, which reported decreased level of sexual reproduction at range limits (Dorken and Eckert 2001; Tremblay et al. 2002; Beatty et al. 2008), reduced seed production and fertility (Pigott and Huntley 1978; García et al. 2000; Sugiyama 2002; Jump and Woodward 2003; Angert 2006) and in offspring number (Ontiveros and Pleguezuelos 2003; Hassall et al. 2006).

Our results show that amount of fruit production - although it differs along the gradient - is less a concern, than the propensity to reproduce. This is especially true for alpine species which, while maintaining a relatively stable fruit production along the gradient, are those having the most marked variation in the propensity to reproduce. On the one hand, this result confirms a series of works carried

out on ectotherms animals, birds, and plants (reviewed in Catalan et al. 2017) that indicate lower investment in reproduction as a characteristic of alpine species. On the other, this phenomenon seems to confirm what Morin et al. (2007) proposed, i.e., the cause of species limitation lie in the incomplete production of fruits because of incomplete ripening.

In our study, reduced fruits-onset is unlikely to be explained by incomplete ripening. In fact, time required from flower-onset to seed production did not vary across our thermal gradient. Thermal environment seems to be ineffective in explaining ripening time, as well as genetics, indicating that along an elevational gradient there is no specific directional selection in favour of short reproduction time. In line, strong species variation occurred ranging from *Erophila praecox* (445 m a.s.l.) able to produce ripe fruits in less than 20 days to *Brabarea vulgaris* (540 m a.s.l.) requiring up to 100 days, with a median required time of ~ 45 days across species. The great variability within the same elevational range indicates that other factors than elevation are affecting species ripening time. This can have profound impact along an elevational gradient allowing some species migrating up-ward and constraining other. Overall, growth season at our highest site was of ~ 200 days resulting in enough time for fruit ripening for any of our species, increase in elevation can have dramatic consequences especially whether plants species are unable of plastic response (e.g., shortening reproductive time, see next section).

Causes for reduced reproduction are still unclear. Within the plants producing flowers the majority produced ripe fruits (>75%) therefore, reduced pollinator service (Moeller et al. 2012), herbivory (Speed et al. 2010) or increased abortion following higher or lower temperature (Morrison and Stewart 2002) seem unlikely to explain the variation in fruit set along the gradient. However, number of plants which did not accomplished reproduction was like the number which died after flower-onset. Consequently, mortality rather than specific reproductive limitations seem to drive the variation in fruit-set along the altitudinal gradient. Open questions remain on the environmental

effects on the quality of offspring produced (e.g., percentage of ripening fruits, number of seeds and endosperm quality).

Phenological plasticity

Our results identified environment as the only driver of flowering onset. Reduction in mean temperature, as simulated by our transplant experiment, resulted in later flowering time for plants species growth under higher (i.e., colder) climate, independently from their origin. Our results are in line with previous studies, which reported environmental-induced effects in alpine species, like earlier flowering under warmer-conditions (Scheepens and Stöcklin 2013; Frei et al. 2014; Schmid et al. 2017; Bucher and Römermann 2020). However, we do not support others works, which reported high levels of photoperiodic induced flowering (e.g., Keller and Körner 2003), which should have resulted in a significant effect of origin in our analysis. We can state that within a phylogenetic and evolutionary framework, there is no directional selection for the timing of flower-onset. A possibility is that flowering behaviour is linked with specific micro-climatic conditions, require specific reproductive size (e.g., Lacey 1986; Wesselingh et al. 1997) or being related to specific life-history strategies (Bucher and Römermann 2020).

As a consequence, the observed variation in reproduction was not a result of phenological behaviour hence phenotypic plasticity will not be able to improve plants performance along the gradient. From a range-limits perspective, this means that low elevation species migrating to high elevation could be potentially affected by two main problems: i) frost and drought damage or ii) season length. Since plastic response seem not to be highlighted as a general trend, and plants are triggered to flower only via environmental-induced factors, lowland species migrating upwards are likely to postpone their flowering time. Consequently, plants species can start flowering later in the season, having by consequence not enough time to fully accomplish their reproductive cycle. On the other side, later flowering increases the risk of early freezing events which can be accompanied by

frost-drought resulting in frost damage to plants or reproductive organs, reducing reproductive output and/or its quality. On the contrary, high elevation species migrating at low elevation should anticipate their flowering time via warmer climate. This seem less problematic since alpine plants can be protected by summer drought/heat; however, this can alter exposure of inflorescences to later frost events or reducing reproductive output via lower pollinator service. Since flowering time is induced by temperature, alpine species have the potential to migrate up-wards in a warming-scenario, if seeds dispersal is not limited. As conclusion, the role of phenological plasticity on range size is highly species-specific and not a trait which can constraints or promote expansion in a general way.

Cost of reproduction

We show that alpine species can reproduce at smaller sizes compared to lowland plants, suggesting a selective role in reproductive size. As the elevation increases, both for plants origin and elevation of transplant sites, the reproductive size decreases. Plastic response (lack of G × E interaction) was detected only in reproductive height, which is likely to be a consequence of high-elevation environment (e.g., strong wind and cooler temperature) on lowland plants, which often resulted in broken inflorescence (personal observation, A. Maccagni). Therefore, smaller reproductive size is likely to be genetically integrated trait, which characterize high- and low- elevation species. Our results support findings of works on latitudinal (e.g., Li et al. 1998) or elevational (e.g., Halbritter et al. 2018) gradients, which observed reduction in size and size at reproduction. Size threshold for reproduction have been reported in plants (e.g., Bonser and Aarssen 2009), consequently the genetic integration of reduced reproductive size can be a result of evolutionary adaptation. Some studies reported that delaying reproduction can be advantageous whether plants reproduce at larger size since it is associated with more and better fruits quality (Silvertown 1983; Schmid et al. 1995; Sletvold 2002). However, in alpine environment reproducing at larger size may not be compatible with its restricted seasonal length. Achieving sexual maturity at smaller size (i.e., early reproduction) can be

advantageous when the loss of demographic fitness due to lower fruit-set is compensated by the long-term gain in fitness, which will be achieved by reproducing in a shorter period of time. Consequently, smaller size in alpine species may not be just a mechanism to exploit the favourable thermic-microclimate at high-elevation (Körner 2003) but could also be the result of an adaptation to compete with the short season. As a conclusion, we suggests that reproductive threshold is under selection across the elevational gradient, promoting bigger individual at low elevation where the season is longer (with higher seed production) and smaller but fast reproducing ones at higher elevation under the constraints of shorter reproductive time (but with fewer seeds).

Our results indicate that the larger is the size at the time of reproduction, the greater is the amount of fruits produced. However, alpine species show the opposite phenomenon, with higher reproductive output at smaller size. This result should be considered in relation to the ability of overwinter survival, which i) was not influenced by the variation in reproductive size, but only by the reproduction itself and ii) was higher in alpine species. What do we know about these traits? First, reproduction is known to influence the resource-allocation in other growth components, e.g., growth reduction of 24% (Méndez and Obeso 1993), or survival (Doust, 1989; Obeso, 1993). Second, alpine species are known to have higher resource allocation to roots, which can act as storage organs (Körner 2003), and that their growth rate is reduced as reproduction increases (Maccagni and Willi 2020, Chapter 3). What seems to emerge here is a variation in resource allocation strategy that differs between high and low elevation plants species. At low elevation, production is favoured, with larger and more productive plants, but whose reproductive cost is higher (i.e., higher over-winter mortality), probably due to a lower investment in storage. In opposition, at higher elevation the strategy is to favour a reduced fruit-production, but which can be maintained on the long term both by high probability of reproducing during the year (given the lowest reproductive threshold) and the highest probability of surviving (and reproducing the following year), which can be the result of resources drained from reproduction to the roots (i.e., storage). Consequently, cost of reproduction and

resource-allocation can potentially influence the shape of species distribution both via reproductive load and overwinter survival.

CONCLUSION

Our study highlights that reproduction differs between species adapted to high- and low-elevation environments. Reproduction is optimal the closer the species are to the habitat in which they are supposed to be. In particular, propensity of fruits production (rather than amount of fruits) seems to be the most limiting factors for up- and low-range expansion. Most notably, date of flowering shows little phenotypic plasticity, a response to the different environments, suggesting a poor role in defining range-limits on the one hand, and unable to buffer against future climate-change on the other hand. To conclude, we observe a divergent reproductive-strategy where, at low elevation, plants reproduce at larger sizes, which results in greater fruit production, but at the cost of increased mortality in the following year; while the opposite applies to alpine species.

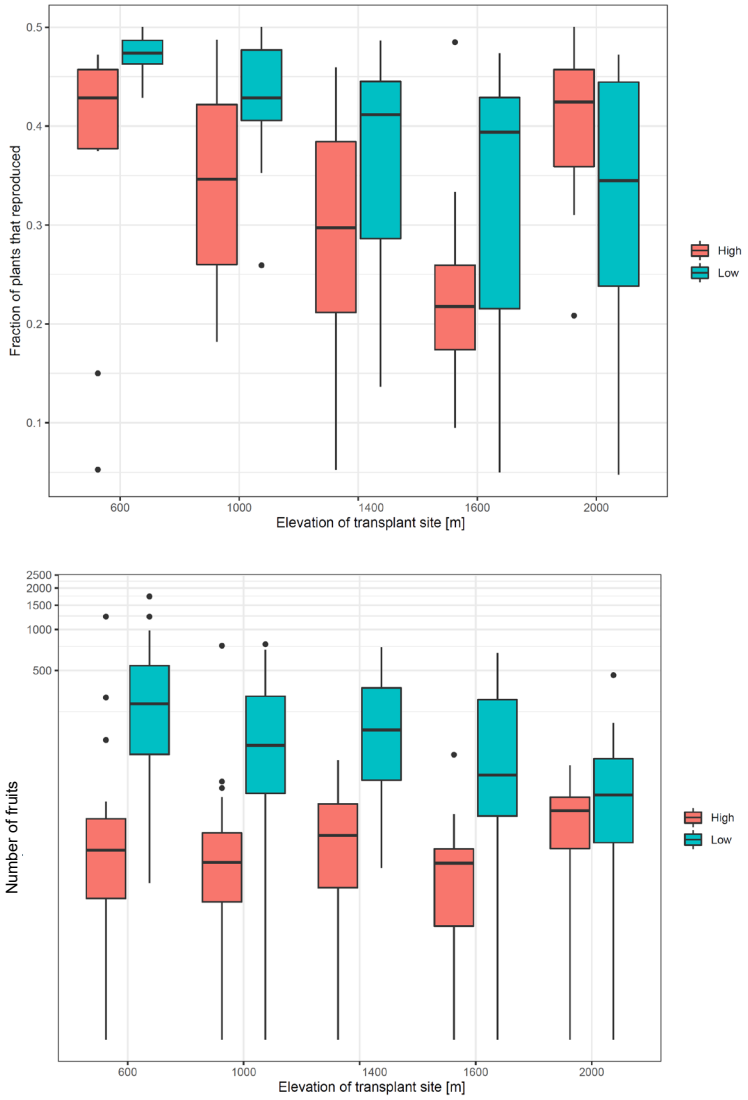

Figure 1 Variation in reproduction between high and low elevation species along the environmental gradient. *Top* Ratio of reproducing plant, *Down* Average number of fruits produced along the elevational gradient. High elevation species are defined as median elevation higher than 1400 m a.s.l.

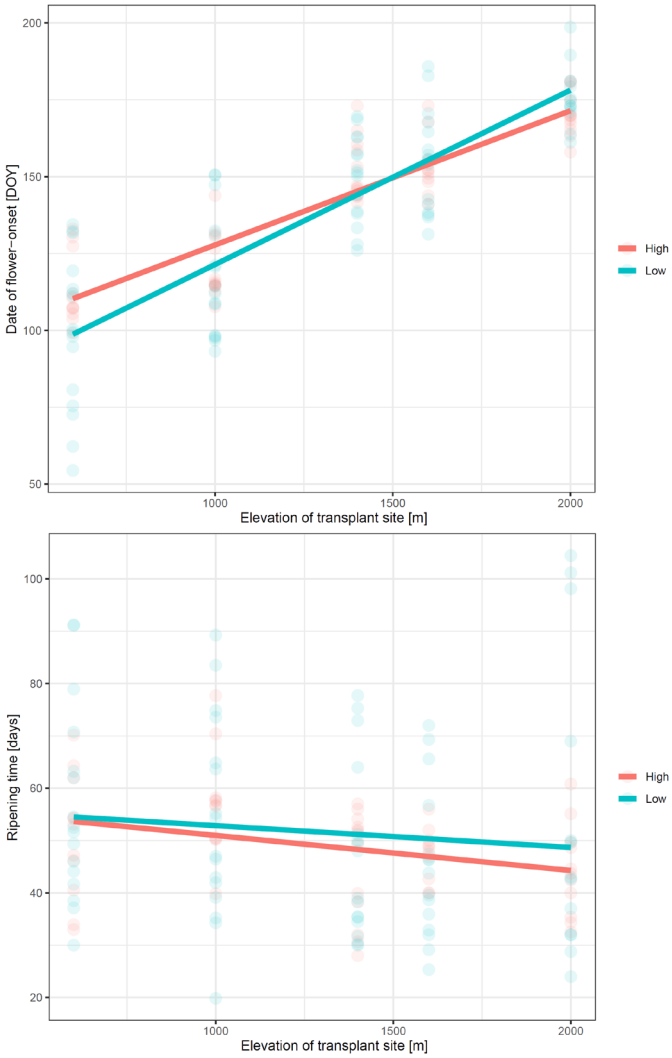

Figure 2 *Top* Date of flower onset (in day of the year, doy). *Down* Variation in ripening time along the elevational gradient. High elevation species are defined as median elevation higher than 1400 m a.s.l.

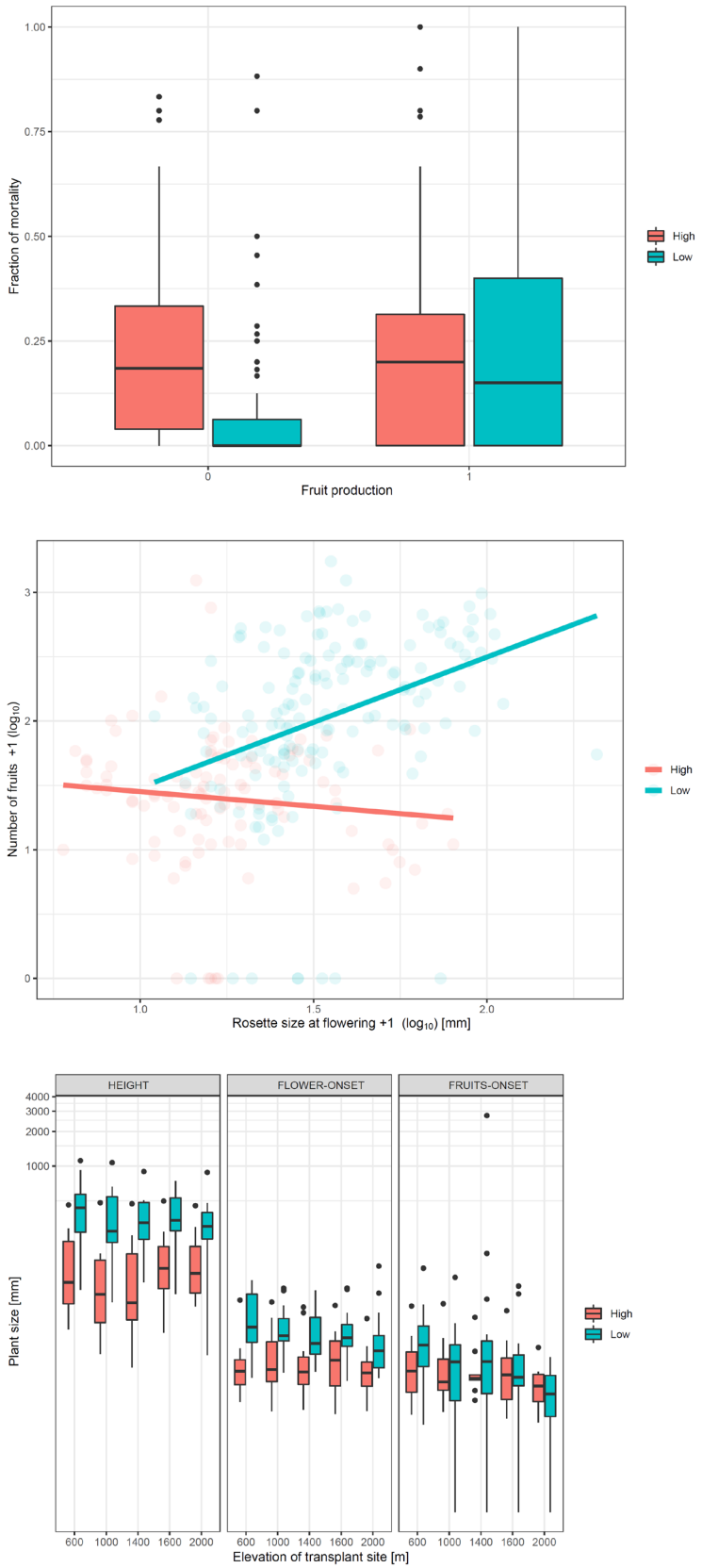

Figure 3 Cost of reproduction. *Top* Relationship between overwinter mortality and effective reproduction (i.e. production of ripe fruits), *Center* Relationship between fruit production and size during flowering-onset. *Down* Variation in reproductive size along the gradient.

Table 1 Location and thermal characterization of the common gardens

Site	Elevation	Latitude	Longitude	Season	Start date	Days	Mean (±SD)
Böfeli	601 m asl	46.87178	9.51882	Growing 2018	10 Oct.	63	8 ± 6
				Winter 2018-19	12 Dec.	41	0 ± 3
				Growing 2019	22 Jan.	324	13 ± 8
				Winter 2019-20	12 Dec.	112	8 ± 9
				Overall			**11.0 ± 8.5**
Arella	997 m asl	46.8738	9.50872	Growing 2018	26 Sept.	78	9 ± 7
				Winter 2018-19	13 Dec.	96	0 ± 1
				Growing 2019	19 Mar.	268	12 ± 9
				Winter 2019-20	12 Dec.	112	7 ± 9
				Overall			**9.7 ± 8.8**
Nesslaboda	1'395 m asl	46.86922	9.49018	Growing 2018	20 Sept.	57	11 ± 6
				Winter 2018-19	16 Nov.	170	1 ± 4
				Growing 2019	05 May	221	11 ± 9
				Winter 2019-20	12 Dec.	111	5 ± 8
				Overall			**7.8 ± 8.6**
Fontanulliaris	1'610 m asl	46.87768	9.49451	Growing 2018	12 Sept	103	7 ± 7
				Winter 2018-19	24 Dec.	132	1 ± 3
				Growing 2019	05 May	221	10 ± 8
				Winter 2019-20	12 Dec.	112	5 ± 8
				Overall			**7.2 ± 8.2**
Neusäss	1'998 m asl	46.88786	9.48949	Growing 2018	14 Aug	74	11 ± 7
				Winter 2018-19	27 Oct	192	0 ± 3
				Growing 2019	07 May	188	9 ± 8
				Winter 2019-20	11 Nov.	159	1 ± 5
				Overall			**5.4 ± 7.7**

Table 2: Mixed-effects model testing for effect of origin and environment on flowering and ripening probability and reproductive output. Origin was previously $\log_{10}$ and describe the median elevation of species occurrence, environment was the elevation of the common garden. Flowering and ripening are binary variables (1: flowering/ripening, 0: non-flowering/ripening; at individual level). Reproductive output was is the mean number of fruits produced per species. Predictors variables were mean centred to 0 and scaled to unit variance to improve model convergence

	Intercept	Origin	Environment	Origin × environment
Flowering	1.071	**-0.442**	**-0.626**	**0.721**
HDI 90%CI	[-0.011, 2.056]	**[-0.794, -0.064]**	**[-0.731, -0.524]**	**[0.623, 0.828]**
	0.942	0.974	1	1
Ripening	0.333	**-0.350**	**-0.528**	**0.422**
HDI 90%CI	[-0.428, 0.868]	**[-0.585, -0.098]**	**[-0.605, -0.454]**	**[0.345, 0.496]**
	0.793	**0.992**	**1**	**1**
Reproductive output	75.261	-0.103	-0.207	**1.532**
HDI 90%CI	[-12.074, 167.145]	[-1.614, 1.549]	[-1.652, 1.235]	**[0.062, 2.889]**
	0.925	0.545	0.591	0.958

Reported values are the median of the posteriors and the 90% credible interval from the high-density interval. **Bold** indicate significant effects.

Table 3.1: Effect of origin (median elevation of species), environment (elevation of transplant site), and their interaction (plasticity) on flowering time. Origin was $\log_{10}$ transformed, mean centred and scaled to unit variance. Day of flowering is the date of flower-onset based on families mean across blocks within sites and centred to mean 0 and unit variance to help model convergence. Families nested within population and species and sites were crossed random effects.

	Intercept	Origin	Environment	Origin × environment
Date of flowering	0.12	-0.028	**0.772**	-0.055
HDI 90%CI	[-0.328; 0.551]	[-0.312; 0.219]	**[0.652; 0.901]**	[-0.153; 0.048]
	0.679	0.583	1	0.841
Day to flowering (winter corrected)	0.082	0.04	**-0.558**	-0.019
HDI 90%CI	[-0.617, 0.653]	[-0.125, 0.238]	**[-0.590, -0.526]**	[-0.049, 0.014]
	0.586	0.649	1	0.819

Reported values are the median of the posteriors and the 90% credible interval from the high-density interval. **Bold** indicate significant effects.

Table 3.2: Mixed-effects model testing for effect of origin and common garden on ripening time. Days for ripening reflect the amount of days required from first flower occurrence to first ripe fruit. 'CV' reflect the coefficient of variation (SD/Mean). Reproduction time was analysed at family level, while CV at the species level for a reliable estimation of SD. Predictors and response variables were mean centred to 0 and scaled to unit variance to improve model convergence. Day for ripening and elevation were additionally $\log_{10}$ transformed to improve normality. Elevation reflect the median occurrence of each species, and site is the elevation of common garden.

	Intercept	Origin	Environment	Origin × environment
Days for ripening (days)	0.123	-0.11	-0.144	-0.038
HDI 90%CI	[-0.389, 0.650]	[-0.614, 0.395]	[-0.277, 0.008]	[-0.132, 0.056]
	0.653	0.65	0.942	0.765
Days for ripening (CV)	0.170	0.153	0.025	0.168
HDI 90%CI	[-0.286, 0.580]	[-0.436, 0.819]	[-0.147, 0.198]	[-0.025, 0.380]
	0.751	0.685	0.601	0.908

Reported values are the median of the posteriors and the 90% credible interval from the high-density interval. **Bold** indicate significant effects.

Table 4: Bayesian mixed-effects model testing for effect of common gardens on size at reproduction. Size at flowering, ripening and elevation were log_{10}-transformed (+1) and centred to mean 0 a unit standard deviation. Elevation reflect the median elevation of occurrence for the species, it was log_{10}-transformed and centred prior analysis. Site was the mean centred elevation of the common garden.

	Intercept	Origin	Environment	Origin × environment
Size at flowering time	0.176	**-0.386**	**-0.176**	0.074
HDI 90%CI	[-0.397, 0.753]	**[-0.733, -0.019]**	**[-0.323, -0.041]**	[-0.007, 0.154]
	0.697	**0.931**	**0.973**	0.946
Size at ripening time	0.083	-0.142	**-0.099**	0.092
HDI 90%CI	[-0.622, 0.881]	[-0.502, 0.225]	**[-0.209, -0.011]**	[-0.090, 0.299]
	0.57	0.743	**0.972**	0.85
Height at ripening time	0.135	**-0.649**	-0.036	**0.062**
HDI 90%CI	[-0.497, 0.708]	**[-1.225, -0.031]**	[-0.117, 0.036]	**[0.004, 0.112]**
	0.635	**0.953**	0.793	**0.974**

Bold highlight significant effects based on the 90% credible interval of the highest density interval of posterior distributions. Reported coefficients reflects the posterior median.

Table 5: Mixed-effects model testing for effect of reproduction, size at reproduction (i.e., flowering, and ripe-fruit) and elevation of origin to over-winter mortality. Flowering and ripening were coded as binary outcome (0/1). Posterior means are given relative to the baseline of non-flowering and non-fruiting (i.e., 0). Size reflect the length of the longest leave at the phenological stage. Size at flowering, ripening and elevation were log_{10}-transformed and centred prior analysis.

	Intercept	Flowering	Ripening	Origin	Origin × flowering	Origin × ripening
Over-winter mortality	**-2.760**	**0.860**	**0.628**	0.878	-0.488	**-0.616**
HDI 90%CI	**[-3.88, -1.62]**	**[0.12, 1.56]**	**[0.05, 1.19]**	[-0.13, 1.90]	[-1.28, 0.23]	**[-1.216; -0.036]**
	99.9	96.63	95.63	92.13	87	95.53
	Intercept	Size at flowering	Size at ripening	Origin	Origin × size at flowering	Origin × size at ripening
Over-winter mortality	**-1.928**	0.077	-0.509	0.203	0.180	-0.363
HDI 90%CI	**[-3.21, -0.67]**	[-0.70, 0.86]	[-1.28, 0.27]	[-1.01, 1.58]	[-0.76, 1.18]	[-1.55, 0.70]
	98.5	56.67	85.6	62.1	63.37	71.47

Bold highlight significant effects based on 90% high-density credible interval.

Table 6: Mixed-effects model testing for effect of size at reproduction, origin and their interactions to reproductive output.

	Intercept	Size at flowering	Size at ripening	Origin × size at flowering	Origin × size at ripening
Reproductive output	-0.009	**0.365**	**0.112**	**-0.149**	0.077
HDI 90%CI	[-0.767, 0.698]	**[0.257, 0.468]**	**[0.027, 0.203]**	**[-0.260, -0.045]**	[-0.005, 0.170]
	0.509	1	0.983	0.982	0.932

Reported values are the median of the posteriors and the 90% credible interval from the high-density interval. **Bold** indicate significant effects.

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CONCLUSIONS

Some species are more common than others or they occur where others do not. These simple, but fascinating biological phenomena have motivated my research in the past four years. In this thesis, I wanted to detect the traits that allowed the colonization of alpine environments and that distinguish high- from low- elevational plants species. Furthermore, I wanted to explore the extent to which the thermal environment and genetic constraints play a role in shaping elevational distribution in middle-European Brassicaceae along an elevational gradient.

In **Chapter 1**, I asked what the traits were that systematically differed between high- and low-elevation species and whether they were linked by a trade-off. I raised plants of 100 species in climate chambers under three thermal regimes, and I measured a number of ecologically relevant traits: aspects of the growth trajectory, leaf functional traits and thermal resistance traits. The results showed that Alpine species could be characterised best by rapid growth under warm conditions, while low-elevation species had greater cold tolerance; in contrast, neither leaf functional traits nor thermal resistance traits were of any importance. Furthermore, growth rate under warm conditions and cold tolerance were found to be linked by a negative correlation, suggesting the existence of a genetic trade-off capable of limiting adaptation of the thermal niche and consequently limiting elevational range expansion.

Species do not only differ in where occurrence ends, they also differ in the size of generally occupied space; they differ in range size. The determinants of range size was the focus of **Chapter 2**. I estimated the importance of phenotypic elasticity and thermal performance breadth on the elevational range width of 100 species. Results failed to support a link between range size and thermal tolerance. However, a strong negative link

between temporal variation in the thermal regime experienced across a species actual range and elasticity was supported, which indicates that increased thermal variability selects against tolerance and promotes thermal specialisation.

In **Chapter 3**, I tested whether alpine species were adapted to their macroclimate. Specifically, along a transect on a mountain slope spanning 1400m in elevation, 30 different Brassicaceae differing in elevational distribution were cultivated at 5 sites and their growth, survival and lifetime performance was estimated. The results supported a generally better performance of species when the difference in elevation between transplantation site and elevation of origin was lower, supporting macroclimate adaptation. However, analyses on the two performance components of growth and survival were not so relevant in causing this pattern. No link between mortality and specific temperature regimes was found. And, alpine species grew faster under low- compared to high-elevation conditions, suggesting incomplete thermal adaptation.

A decline in reproductive output from the centre to the periphery of the range can be another explanation for range limits. In **Chapter 4,** I investigated whether there was an aspect of reproduction that was particularly constraining and whether there were costs associated with reproduction. Data of the experiment described under Chapter 3 was analysed, with a focus on the phenology of reproduction. Results indicated that the probability of producing fruits was reduced as the distance in elevation between transplant site and origin of the species increased, supporting that the most limiting performance aspect for range limits is reproduction. I also found that reproduction reduced over-winter survival in lowland species, and fruit production is affected by the size of inflorescences, indicating the existence of a trade off in resource allocation to reproduction versus survival.

What characterizes alpine Brassicaceae species? My results indicate that alpine species do not have a higher (or lower) resistance to extreme temperatures, but rather they differ in the way their growth responds to temperature. Specifically, I detected that alpine species grow faster, and in particular, they respond well to warmer temperatures. The more rapid growth under warm conditions, however, does not translate in a more rapid reproductive development, in early flowering and/or early ripening of fruits; both timing of flowering and time required for fruit ripening was indistinguishable between high- and low-elevation species. In contrast, fruit production, although relatively constant at different altitudes, was lower in alpine species, indicating a reduced reproductive effort. Alpine species, at least in the first year, showed a lower survival, but this lower survival was more pronounced at lower altitudes, indicating adaptation to macroclimatic conditions. Nevertheless, mortality did not depend on specific temperatures, suggesting that this adaptation is related to other factors and/or an interaction between them and temperature.

What are the consequences of temperature? Temperature has always been considered fundamental in shaping the distribution of species and it is one of few parameters that define elevational gradients. This has led many past studies to explore species (elevational) ranges and their limits in the light of variation in thermal resistance and differences in physiological optima. It is indisputable that temperature influences the physiology of species and contributes to their limitation. However, our results show that, at least for thermal variation along an elevational gradient, the distribution of herbaceous species is not explained by higher or lower resistance to thermal conditions. Rather it is the way in which the growth trajectory of species responds to temperature. Furthermore,

temperature seems to have caused the adaptation of species, at the physiological level (e.g., response of growth to heat). And some adaptation may have evolved in response to temperature altering other abiotic aspects (e.g. reducing the growing season). However, there is still the possibility that species of low and high elevations differ in resistance as the response to selection may involve some degree of non-convergence within species groups; several paths of adaptation may be possible and achieved with varying ease among species. The resulting heterogeneity in adaptive solutions among species may have blurred the detectability of a general pattern, due to my experimental designs. This emphasizes that more attention should be paid in the interpretation of results along short thermal gradients when variables that are intrinsically correlated do not necessarily have the assumed effect.

What constrains the adaptation of species? As has long been hypothesized, adaptation to elevation seems limited by trade-offs. These seem to manifest themselves on several axes. First, different environments – high versus low elevation – select for different traits, fast growth under warmth versus high tolerance to frost. These traits are involved in a genetic trade-off that is likely to reinforce this adaptive distinction by limiting or preventing the evolution of the elevational niche. Second, a trade-off in the allocation of resources exists, particularly between reproduction versus growth and survival, but the details of the trade-off differ among low- and high-elevation species. For high-elevation species, the trade-off is more about speed of growth versus reproductive output. For high-elevation species, the trade-off concerns reproductive output versus survival after reproduction. Third, greater phenotypic elasticity in trait expression and in thermal tolerance is not related with a wider elevational niche, but rather more elasticity limits

species in occurring in thermally more variable environments. Or, in other words, thermally more variable environments favour the evolution of thermal specialization. I conclude that that these three trade-offs are the reason why species perform best under typical elevational conditions but fail under un-typical elevation, as found in the transplant experiment, and in line with where we find the species in nature.

Future directions and closing notes

This research has contributed to a better understanding of why species have limited distributions along an elevational gradient, and in particular the contribution of temperature in causing range limits. On the one hand, I found support for the prediction that trade-offs are limiting the evolution of the niche, on the other hand, the research highlights that the role of temperature needs to be reassessed. Adaptation to temperature should not be studied in terms of differences in thermal resistance, but rather in terms of how species react to temperature in growth and in more generally, with a focus on to growth and maintenance versus reproduction.

In light of these facts, more research is needed to elucidate some fundamental aspects. First, although my analysis involved 100 different species, they represented a limited sample of plant diversity as they were all of one plant family and had experienced a similar spatial evolutionary context (the Central European Alps). More work is needed that includes alpine species of more diverse taxonomic background and from different latitudes to confirm whether results found in my thesis can be generalized to the global alpine ecosystem. Concerning the purely abiotic aspects, a clarification of the fundamental niche would be desirable through multifactorial experiments aimed at

understanding the role of the various abiotic components and their interactions, in particular aspects such as frost drought and the effect of prolonged winter (long period below the snow cover), on performance. Finally, a great focus should be given to the causes that lie behind the different allocation of resources to growth and maintenance versus reproduction, which environmental conditions select for this variation and what are the consequences for the long-term dynamics of populations. Finally, it is essential to develop evolutionary experiments aimed at verifying whether the trade-offs I highlighted have an effective role in limiting adaptation to elevation (and niche expansion) and what the consequences on fitness are.

SUPPELEMENTARY MATERIAL

Supplementary material - A1 (Chapter 1): List of species used

List of taxa (species and subspecies) used in the study. Names of species are according to www.infoflora.ch v. 2020, or www.brassibase.cos.uni-heidelberg.de v. 2020. Information on the sampling sites includes: the locality with the abbreviation for Canton, the coordinates (X, Y, CH1903 / LV03), the date of sampling, the internal code (sample_ID, University **of Basel, Plant Ecology and Evolutionary group**), the round of sowing plant material was assessed, and the predominant elevational distriubtion of the species, based on Flora Alpina (Aeschimann et al., 2004).

Species name (InfoFlora, 2020)	Species name (BrassiBase, 2020)	Locality (Canton)	CoordinateCH_X	CoordinateCH_Y	Sampling date	Sample ID	Sowing		Elevational class
Alliaria petiolata		Neuchâtel (NE)	561591	205541	30.06.2015	0014	S1	S2	low
Alliaria petiolata		Birsfelden (BL)	614764	266636	06.07.2015	0015	S1	S2	low
Alyssoides utriculata		Saillon (VS)	580227	113193	14.06.2016	0035	S1	S2	low
Alyssoides utriculata		Salvan(VS)	567965	107502	14.06.2016	0036	S1	S2	low
Alyssum alyssoides		Mt-Noble (VS)	598143	118772	22.06.2016	0040	S1	S2	low
Alyssum alyssoides		Zermatt (VS)	624175	97320	06.08.2016	0097	S1	S2	low
Alyssum argenteum		Vollèges (VS)	576478	103311	06.08.2016	0091	S1	-	low
Alyssum montanum		Kleinlützel (SO)	598326	254717	18.06.2015	0008	S1	S2	low
Alyssum montanum		Waldenburg (BL)	620438	246779	21.06.2015	0010	S1	S2	low
Arabidopsis thaliana		Buseno (GR)	728849	125853	05.06.2016	0028	S1	S2	low
Arabidopsis thaliana		Basel (BS)	611323	270231	10.05.2017	0209	S1	S2	low
Arabis alpina subsp. alpina		Medels (GR)	704617	159917	10.08.2016	0103	S1	S2	high
Arabis alpina subsp. alpina		Wildhaus Alt St. Johann (SG)	745411	234162	15.09.2016	0151	S1	S2	high
Arabis auriculata		Rochefort (NE)	550864	203089	29.07.2016	0128	S1	S2	low
Arabis bellidifolia subsp. stellulata	Arabis stellulata	Val Müstair (GR)	828677	159977	29.08.2017	0228	S1	S2	high
Arabis bellidifolia subsp. stellulata	Arabis stellulata	Obergoms (VS)	672460	147169	28.09.2017	0237	S1	S2	high
Arabis caerulea		Zermatt (VS)	628345	96957	13.09.2016	0147	S1	S2	high
Arabis caerulea		Lischana / Scuol (GR)	821865	182995	19.09.2016	0162	S1	S2	high
Arabis ciliata		Zermatt (VS)	627610	95860	27.08.2016	0144	S1	S2	high
Arabis ciliata		Capriasca (TI)	717931	106862	12.06.2017	0211	S1	S2	high
Arabis collina		Pazzallo (TI)	716881	92806	10.07.2017	0215	S1	S2	low
Arabis nova		Grächen (VS)	629868	115937	15.07.2016	0094	S1	S2	high
Arabis nova		Poschiavo (GR)	802776	132669	20.07.2016	0111	S1	S2	high
Arabis rosea		Orbe (VD)	530723	175380	28.07.2016	0127	S1	S2	low
Arabis rosea		Neuchâtel (NE)	562486	205572	19.07.2017	0218	S1	S2	low
Arabis sagittata		Rovio (TI)	720922	88939	09.07.2015	0016	S1	S2	low
Arabis sagittata		Montcherand (VD)	527776	175762	28.08.2016	0138	S1	S2	low
Arabis serpillifolia		Kandersteg (BE)	617371	146771	12.08.2016	0135	S1	S2	high
Arabis subcoriacea	Arabis soyeri subsp. subcoriacea	Olivone (TI)	705007	156062	04.08.2016	0101	S1	S2	high
Arabis subcoriacea	Arabis soyeri subsp. subcoriacea	Davos (GR)	781892	186834	19.07.2016	0110	S1	S2	high
Arabis turrita	Pseudoturritis turrita	Dorenaz (VS)	569818	110242	24.06.2015	0011	S1	S2	low
Arabis turrita	Pseudoturritis turrita	Castel San Pietro (TI)	722265	79753	09.07.2016	0067	S1	S2	low
Aurinia saxatilis		Grimisuat (VS)	594866	121911	07.06.2016	0025	-	S2	low
Barbarea intermedia		Eggiwil (BE)	628398	190904	19.07.2016	0123	S1	S2	low
Barbarea intermedia		Alpnach (OW)	662034	203445	30.09.2016	0167	S1	S2	low
Barbarea verna		Kloten (ZH)	685568	255345	21.06.2017	0199	S1	S2	low
Barbarea vulgaris		Mendrisio (TI)	721454	85770	09.08.2016	0102	S1	S2	low
Barbarea vulgaris		Hauterive (FR)	575744	179966	23.07.2016	0125	S1	S2	low
Berteroa incana		Gampel (VS)	623277	128518	20.07.2016	0084	S1	S2	low
Berteroa incana		Cugy (FR)	557867	184245	09.08.2016	0133	S1	S2	low
Biscutella laevigata		Poschiavo (GR)	797429	142775	22.08.2016	0116	S1	S2	high
Biscutella laevigata		Olivone (TI)	705860	156026	02.08.2017	0219	S1	S2	high
Bunias orientalis		Villa / Ayent (VS)	598198	125000	20.07.2016	0083	S1	S2	low
Bunias orientalis		Scuol (GR)	817267	186490	11.08.2016	0141	S1	S2	low

Species name (InfoFlora, 2020)	Species name (BrassiBase, 2020)	Locality (Canton)	CoordinateCH_X	CoordinateCH_Y	Sampling date	Sample ID	Sowing		Elevational class
Camelina microcarpa		Mt-Noble (VS)	598139	118776	21.06.2016	0039	S1	S2	low
Capsella bursa-pastoris		Pambio-Noranco (Lugano) (TI)	715433	93240	05.05.2016	0026	S1	S2	low
Capsella bursa-pastoris		Pfungen (ZH)	689611	263695	09.06.2016	0055	S1	S2	low
Capsella rubella		Melano (TI)	719561	87042	27.05.2016	0027	S1	S2	low
Capsella rubella		Fribourg (FR)	578511	184861	15.05.2016	0030	S1	S2	low
Cardamine alpina		Poschiavo (GR)	799654	141514	02.09.2016	0119	S1	S2	high
Cardamine alpina		Bedretto (TI)	673084	147930	28.09.2017	0239	S1	S2	high
Cardamine amara		Dardagny (GE)	489128	116835	17.06.2015	0007	S1	S2	low
Cardamine amara		Poschiavo (GR)	798402	143407	02.09.2016	0118	S1	S2	low
Cardamine asarifolia		Brusio (GR)	807864	128262	05.08.2016	0114	S1	S2	high
Cardamine bulbifera		Castel San Pietro (TI)	722494	79876	14.06.2016	0045	S1	-	low
Cardamine heptaphylla		Mezzovico (TI)	715266	105837	03.06.2017	0206	S1	S2	low
Cardamine hirsuta		Neuchâtel (NE)	561595	205520	28.04.2015	0001	S1	S2	low
Cardamine hirsuta		Zug (ZG)	679912	225784	05.05.2015	0002	S1	S2	low
Cardamine impatiens		Neunkirch (SH)	679282	280541	03.07.2016	0057	S1	S2	low
Cardamine impatiens		Castel San Pietro (TI)	722528	79912	03.06.2017	0207	S1	S2	low
Cardamine kitaibelii		Melano (TI)	720357	87404	07.06.2016	0043	S1	S2	low
Cardamine kitaibelii		Braunwald (GL)	717835	198579	31.07.2016	0080	S1	S2	low
Cardamine matthioli		Turtmann (VS)	619789	127867	28.05.2015	0020	S1	S2	low
Cardamine matthioli		Origlio (TI)	716543	101102	25.05.2017	0212	S1	S2	low
Cardamine pratensis		Rodi (TI)	700313	149468	21.06.2017	0214	-	S2	low
Cardamine resedifolia		Zermatt (VS)	629656	95873	06.08.2016	0095	S1	S2	high
Cardamine resedifolia		Poschiavo (GR)	797461	142862	05.08.2016	0113	S1	S2	high
Cardamine trifolia		Jegenstorf (BE)	606036	212293	11.06.2017	0201	S1	S2	low
Cardamine trifolia		Rossinière (VD)	571740	145371	30.06.2017	0203	S1	S2	low
Cardaminopsis arenosa subsp. arenosa	Arabidopsis arenosa subsp.arenosa	Fribourg (FR)	578953	183152	16.06.2015	0006	S1	S2	low
Cardaminopsis arenosa subsp. arenosa	Arabidopsis arenosa subsp.arenosa	Airolo (TI)	691068	153647	29.06.2015	0013	S1	S2	low
Cardaminopsis arenosa subsp. borbasii	Arabidopsis arenosa subsp. borbasii	Eggiwil (BE)	628591	190689	20.07.2016	0124	S1	S2	low
Cardaminopsis arenosa subsp. borbasii	Arabidopsis arenosa subsp. borbasii	Muriaux (JU)	564224	231847	10.08.2016	0134	S1	S2	low
Cardaminopsis halleri	Arabidopsis halleri	Beride (TI)	708081	95566	12.06.2016	0044	S1	S2	high
Cardaminopsis halleri	Arabidopsis halleri	St. Moritz (GR)	785255	152806	10.08.2016	0115	S1	S2	high
Cardaria draba	Lepidium draba	Uvrier (VS)	598373	122127	08.07.2016	0062	S1	S2	low
Clypeola jonthlaspi		Sion gare (VS)	593823	119521	07.05.2016	0023	S1	S2	low
Cochlearia pyrenaica		Plaffeien (FR)	593454	169104	12.09.2016	0160	S1	S2	high
Cochlearia pyrenaica		Kandersteg (BE)	617835	147964	28.07.2017	0226	S1	S2	high
Descurainia sophia		Sion (VS)	593080	118720	06.06.2016	0024	S1	S2	low
Diplotaxis tenuifolia		Turtig (VS)	626679	128123	03.08.2016	0089	S1	S2	low
Diplotaxis tenuifolia		Arzo (TI)	717292	82151	27.07.2016	0100	S1	S2	low
Draba aizoides		Trimbach (SO)	634083	247700	27.05.2016	0033	S1	S2	high
Draba aizoides		Zermatt (VS)	626380	92415	28.08.2016	0145	S1	S2	high
Draba dubia		Quinto (TI)	695022	154237	19.07.2016	0075	S1	S2	high
Draba dubia		Zermatt (VS)	626542	92458	14.09.2016	0150	S1	S2	high
Draba fladnizensis		Scuol (GR)	814057	189300	21.07.2017	0225	S1	S2	high
Draba fladnizensis		Zermatt (VS)	627711	96727	30.08.2017	0233	S1	S2	high
Draba hoppeana		Zermatt (VS)	628394	96951	13.09.2016	0148	S1	S2	high
Draba hoppeana		Lischana / Scuol (GR)	821857	182969	19.09.2016	0163	S1	S2	high
Draba muralis	Drabella muralis	Maroggia (TI)	718942	88085	15.04.2017	0196	S1	S2	low
Draba muralis	Drabella muralis	Uster (ZH)	699287	244107	21.06.2017	0202	S1	S2	low
Draba nemorosa		Gampel (VS)	624849	128499	18.06.2015	0009	S1	S2	high
Draba nemorosa		Ardez (GR)	812333	184787	14.06.2016	0056	S1	S2	high
Draba siliquosa		Zermatt (VS)	627286	96017	07.08.2016	0081	S1	S2	high

Species name (InfoFlora, 2020)	Species name (BrassiBase, 2020)	Locality (Canton)	CoordinateCH_X	CoordinateCH_Y	Sampling date	Sample ID	Sowing		Elevational class
Draba siliquosa		Pontresina (GR)	797531	143496	04.08.2016	0112	S1	S2	high
Draba tomentosa		Wildhaus Alt St. Johann (SG)	745826	234180	24.08.2016	0142	S1	S2	high
Draba tomentosa		Val Müstair (GR)	827974	159730	29.08.2017	0229	S1	S2	high
Erophila praecox	Draba verna	Fribourg (FR)	578476	185388	17.05.2016	0031	S1	S2	low
Erophila praecox	Draba verna	Origlio (TI)	716594	101509	21.04.2017	0204	S1	S2	low
Erophila verna	Draba verna	Zürich (ZH)	683182	250983	29.04.2016	0029	S1	S2	low
Erophila verna	Draba verna	Pambio-Noranco (TI)	715686	93883	09.04.2017	0197	S1	S2	low
Erucastrum gallicum		Hauterive (FR)	575746	179963	27.07.2016	0126	S1	S2	low
Erucastrum nasturtiifolium		Grimisuat (VS)	595950	122730	15.06.2016	0038	S1	S2	low
Erysimum cheiranthoides		St. Moritz (GR)	784896	152459	22.08.2016	0117	S1	S2	low
Erysimum cheiri		Grandson (VD)	539537	184588	07.08.2016	0131	-	S2	low
Erysimum rhaeticum		Erschmatt (VS)	618888	130403	24.07.2016	0087	S1	S2	low
Euclidium syriacum		Äscher Wildkirchli (AI)	749384	238773	27.07.2016	0078	S1	-	low
Fourraea alpina		Arzo (TI)	717154	82402	09.07.2016	0068	S1	S2	low
Fourraea alpina		San Bernardino (GR)	735773	147364	15.08.2017	0221	S1	S2	low
Hesperis matronalis		Claro (TI)	721419	124864	11.08.2016	0105	S1	S2	low
Hesperis matronalis		Castel San Pietro (TI)	722289	79996	22.08.2016	0108	S1	S2	low
Hirschfeldia incana		St. Gallen (SG)	745409	254139	22.09.2016	0154	S1	S2	low
Hirschfeldia incana		Alpnach (OW)	667905	203028	07.09.2017	0236	S1	S2	low
Hornungia petraea		Noiraigue (NE)	546256	200495	25.05.2016	0032	S1	S2	low
Hornungia petraea		Leuk-Susten (VS)	617923	128537	18.04.2017	0198	S1	S2	low
Hugueninia tanacetifolia	Descurainia tanacetifolia	Evolène (VS)	603630	95100	25.08.2016	0099	S1	S2	high
Hugueninia tanacetifolia	Descurainia tanacetifolia	Bourg St. Pierre (VS)	579084	79819	04.10.2016	0140	S1	S2	high
Iberis saxatilis		Albinen (VS)	615413	131042	06.07.2016	0060	S1	S2	high
Isatis tinctoria		Uvrier / Sion (VS)	598686	121360	13.06.2016	0034	S1	S2	low
Kernera saxatilis		Seewis (GR)	756696	204989	04.07.2016	0065	S1	S2	high
Kernera saxatilis		Pazzallo (TI)	716937	92864	19.06.2017	0213	S1	S2	high
Lepidium campestre		Sion (VS)	592525	119410	26.06.2016	0041	S1	S2	low
Lepidium campestre		Chavornay (VD)	533922	174531	14.07.2016	0121	S1	S2	low
Lepidium virginicum		Sion (VS)	593057	118711	15.06.2016	0037	S1	S2	low
Lepidium virginicum		Chiasso (TI)	722264	77061	26.09.2017	0240	S1	S2	low
Lunaria annua		Castel San Pietro (TI)	722264	79770	18.07.2016	0074	S1	S2	low
Lunaria rediviva		Valcolla (TI)	720988	103824	14.07.2016	0071	S1	S2	low
Lunaria rediviva		Alpstein (AI)	748461	236788	16.09.2016	0153	S1	S2	low
Matthiola valesiaca	Matthiola fruticulosa subsp. valesiaca	Leuk-Susten (VS)	612684	128703	01.07.2016	0058	S1	S2	low
Matthiola valesiaca	Matthiola fruticulosa subsp. valesiaca	Binn - Twingi (VS)	656250	134655	04.08.2016	0090	S1	S2	low
Murbeckiella pinnatifida		Trient (VS)	563730	97869	25.08.2017	0224	S1	S2	high
Murbeckiella pinnatifida		Bourg St.Pierre (VS)	579478	80468	18.08.2017	0232	S1	S2	high
Nasturtium officinale		Novazzano (TI)	720802	77306	27.06.2016	0051	S1	S2	low
Nasturtium officinale		Saillon (VS)	579797	113019	15.07.2016	0082	S1	S2	low
Neslia paniculata		Mont Noble (VS)	599348	116068	25.07.2017	0216	S1	S2	low
Neslia paniculata		Ried-Brig (VS)	643901	130119	11.07.2017	0217	S1	S2	low
Petrocallis pyrenaica		Wildhaus Alt St. Johann (SG)	745826	234192	15.09.2016	0152	S1	S2	high
Petrocallis pyrenaica		Erlenbach i.S. (BE)	607550	171414	17.08.2017	0227	S1	S2	high
Prizelago alpina subsp. alpina	Hornungia alpina subsp. alpina	Rougemont (VD)	582054	145461	30.08.2016	0139	S1	S2	high
Prizelago alpina subsp. alpina	Hornungia alpina subsp. alpina	Davos (GR)	781167	187882	23.09.2016	0166	S1	S2	high
Prizelago alpina subsp. brevicaulis	Hornungia alpina subsp. brevicaulis	Zermatt (VS)	626516	92449	28.08.2016	0146	S1	S2	high
Prizelago alpina subsp. brevicaulis	Hornungia alpina subsp. brevicaulis	Lischana / Scuol (GR)	821861	182962	19.09.2016	0164	S1	S2	high
Rorippa islandica		Hérémence (VS)	594313	111885	11.09.2017	0234	S1	S2	high
Rorippa islandica		Ollon (VD)	571675	130713	06.09.2017	0235	S1	S2	high
Rorippa palustris		Zermatt (VS)	624008	96835	29.09.2016	0158	S1	S2	low

Species name (InfoFlora, 2020)	Species name (BrassiBase, 2020)	Locality (Canton)	CoordinateCH_X	CoordinateCH_Y	Sampling date	Sample ID	Sowing		Elevational class
Rorippa palustris		Molina Buseno (GR)	728687	125431	28.09.2017	0241	S1	S2	low
Rorippa stylosa	Rorippa pyrenaica	Motto Blenio (TI)	718203	143828	04.08.2017	0220	S1	S2	low
Rorippa stylosa	Rorippa pyrenaica	Naters (VS)	642237	132234	01.07.2017	0230	S1	S2	low
Rorippa sylvestris		Kerzers (FR)	580503	204771	13.09.2016	0161	S1	S2	low
Rorippa sylvestris		St. Margrethen (SG)	763628	259144	31.07.2017	0231	S1	S2	low
Sinapis arvensis		Grimisuat (VS)	595005	121820	08.07.2016	0063	S1	S2	low
Sinapis arvensis		Allschwill (BL)	608124	265683	07.06.2017	0208	S1	S2	low
Sisymbrium altissimum		Drône / Savièse	594354	122573	22.07.2016	0086	S1	S2	low
Sisymbrium austriacum		St. Moritz (GR)	784982	152574	03.09.2016	0120	S1	S2	low
Sisymbrium austriacum		Ayent (VS)	598945	125780	20.06.2017	0200	S1	S2	low
Sisymbrium irio		Sion (VS)	594280	119740	03.05.2016	0022	S1	S2	low
Sisymbrium irio		Zürich (ZH)	682792	253196	07.07.2016	0066	S1	S2	low
Sisymbrium officinale		Botyre (VS)	597485	124840	22.07.2016	0085	S1	S2	low
Sisymbrium officinale		Zürich (ZH)	682877	249379	29.06.2016	0092	S1	S2	low
Sisymbrium orientale		Chavornay (VD)	533922	174531	14.07.2016	0122	S1	S2	low
Sisymbrium strictissimum		Scuol (GR)	818795	186661	27.09.2016	0156	S1	S2	low
Thlaspi alliaceum		Bottmingen (BL)	610899	262489	29.05.2015	0003	S1	S2	low
Thlaspi alliaceum		Flaach (ZH)	685513	269933	02.06.2015	0004	S1	S2	low
Thlaspi arvense		Sion (VS)	592520	119405	26.06.2016	0042	S1	S2	low
Thlaspi arvense		Grandcour (VD)	560218	190847	30.06.2016	0054	S1	S2	low
Thlaspi brachypetalum	Noccaea brachypetala	Amsteg (UR)	692138	178151	09.06.2015	0005	S1	S2	high
Thlaspi brachypetalum	Noccaea brachypetala	Escholzmatt (LU)	636902	196739	20.06.2016	0048	S1	S2	high
Thlaspi caerulescens	Noccaea caerulescens	Les Echadex (VD)	506122	152055	26.06.2015	0012	S1	S2	high
Thlaspi caerulescens	Noccaea caerulescens	Gorgier (NE)	546896	198076	10.07.2015	0017	S1	S2	high
Thlaspi perfoliatum	Microthlaspi perfoliatum	Ayent (VS)	597489	124557	28.04.2016	0021	S1	S2	low
Thlaspi perfoliatum	Microthlaspi perfoliatum	Meride (TI)	716550	84397	30.04.2017	0205	S1	S2	low
Thlaspi rotundifolium subsp. corymbosum	Noccaea corymbosa	San Vittore (GR)	725534	128858	14.08.2016	0106	S1	S2	high
Thlaspi rotundifolium subsp. corymbosum	Noccaea corymbosa	Zermatt (VS)	619070	92681	08.09.2016	0243	S1	S2	high
Thlaspi rotundifolium subsp. rotundifolium	Noccaea rotundifolia	Braunwald (GL)	717104	201724	30.07.2016	0079	S1	S2	high
Thlaspi rotundifolium subsp. rotundifolium	Noccaea rotundifolia	Wildhaus Alt St. Johann (SG)	745436	234181	24.08.2016	0143	S1	S2	high
Thlaspi sylvium	Noccaea sylvia	Zermatt (VS)	628599	95709	06.08.2016	0096	S1	S2	high
Turritis glabra		Mont Noble (VS)	600970	115870	19.08.2016	0098	S1	S2	low
Turritis glabra		Tengia (TI)	706887	147659	22.08.2017	0223	S1	S2	low

variable..SSIZ	post.mean	sd	l.95..CI	u.95..CI	pMCMC	sign.
(Intercept)	0.653	0.177	0.316	0.997	0.00	***
scale.median_elevation	−0.026	0.026	−0.076	0.028	0.32	
taxa	0.290	0.045	0.203	0.379	NA	NA
units	0.001	0.000	0.001	0.001	NA	NA

variable..TGER	post.mean	sd	l.95..CI	u.95..CI	pMCMC	sign.
(Intercept)	16.667	83.482	−8.925	53.861	0.842	
scale.median_elevation	0.302	0.381	−0.423	1.076	0.427	
taxa	16.449	4.433	8.409	24.987	NA	NA
sowing_id	35718.242	1440611.933	0.578	2963.021	NA	NA
units	13.911	1.015	11.944	15.880	NA	NA

variable..IGR	post.mean	sd	l.95..CI	u.95..CI	pMCMC	sign.
(Intercept)	0.580	0.011	0.559	0.601	0.000	***
treatmentF	−0.004	0.009	−0.020	0.013	0.635	
treatmentH	−0.008	0.009	−0.026	0.008	0.325	
scale.median_elevation	−0.005	0.007	−0.017	0.008	0.447	
treatmentF:scale.median_elevation	0.007	0.009	−0.010	0.025	0.451	
treatmentH:scale.median_elevation	0.007	0.008	−0.008	0.025	0.389	
taxa	0.001	0.000	0.000	0.001	NA	NA
units	0.003	0.000	0.003	0.004	NA	NA

variable..MGR.log10	post.mean	sd	l.95..CI	u.95..CI	pMCMC	sign.
(Intercept)	0.262	47.308	−1.970	0.633	0.996	
treatmentF	0.007	0.025	−0.045	0.054	0.788	
treatmentH	0.246	0.025	0.191	0.291	0.000	***
scale.median_elevation	−0.026	0.018	−0.064	0.009	0.161	
treatmentF:scale.median_elevation	0.021	0.026	−0.030	0.072	0.410	
treatmentH:scale.median_elevation	0.084	0.026	0.030	0.132	0.002	**
taxa	0.001	0.001	0.000	0.003	NA	NA
sowing_id	1367.670	73250.571	0.001	5.968	NA	NA
units	0.051	0.003	0.044	0.057	NA	NA

variable..(-)XMID	post.mean	sd	l.95..CI	u.95..CI	pMCMC	sign.
(Intercept)	−28.747	239.313	−85.723	34.928	0.904	
treatmentF	0.934	0.471	0.030	1.873	0.047	*
treatmentH	3.112	0.482	2.174	4.024	0.000	***
scale.median_elevation	−0.602	0.431	−1.410	0.253	0.163	
treatmentF:scale.median_elevation	0.167	0.483	−0.824	1.052	0.730	
treatmentH:scale.median_elevation	1.723	0.496	0.740	2.698	0.001	**
taxa	8.006	2.684	3.244	13.175	NA	NA
sowing_id	168537.277	5756236.452	3.073	12797.402	NA	NA
units	17.953	1.304	15.555	20.579	NA	NA

variable..ASYM	post.mean	sd	l.95..CI	u.95..CI	pMCMC	sign.
(Intercept)	1.495	11.298	1.210	2.185	0.895	
treatmentF	−0.063	0.012	−0.088	−0.039	0.000	***
treatmentH	−0.068	0.013	−0.092	−0.043	0.000	***
scale.median_elevation	−0.017	0.019	−0.056	0.020	0.376	
treatmentF:scale.median_elevation	−0.012	0.013	−0.038	0.012	0.341	
treatmentH:scale.median_elevation	−0.060	0.013	−0.086	−0.034	0.000	***
taxa	0.064	0.013	0.041	0.088	NA	NA
sowing_id	509.685	27703.930	0.000	0.836	NA	NA
units	0.012	0.001	0.011	0.014	NA	NA

variable..NLEA.log10	post.mean	sd	l.95..CI	u.95..CI	pMCMC	sign.
(Intercept)	1.074	0.119	0.850	1.311	0.000	***
treatmentF	−0.027	0.012	−0.050	−0.004	0.023	*
treatmentH	0.001	0.012	−0.024	0.023	0.957	
scale.median_elevation	−0.005	0.024	−0.049	0.044	0.839	
treatmentF:scale.median_elevation	−0.004	0.012	−0.026	0.019	0.760	
treatmentH:scale.median_elevation	−0.010	0.012	−0.031	0.015	0.422	
taxa	0.130	0.024	0.087	0.176	NA	NA
units	0.006	0.001	0.005	0.007	NA	NA

variable..LA.log10	post.mean	sd	l.95..CI	u.95..CI	pMCMC	sign.
(Intercept)	2.527	1.636	2.055	2.998	0.123	
treatmentF	−0.072	0.022	−0.114	−0.026	0.001	**
treatmentH	−0.113	0.023	−0.158	−0.069	0.000	***
scale.median_elevation	−0.155	0.035	−0.224	−0.089	0.000	***
treatmentF:scale.median_elevation	0.014	0.023	−0.031	0.059	0.528	
treatmentH:scale.median_elevation	−0.050	0.022	−0.094	−0.007	0.025	*
taxa	0.205	0.039	0.137	0.281	NA	NA
sowing_id	10.760	331.475	0.000	0.483	NA	NA
units	0.036	0.003	0.030	0.041	NA	NA

variable..SLA	post.mean	sd	l.95..CI	u.95..CI	pMCMC	sign.
(Intercept)	24.974	10.316	18.747	30.676	0.015	*
treatmentF	−3.191	0.749	−4.577	−1.668	0.000	***
treatmentH	3.131	0.780	1.718	4.691	0.000	***
scale.median_elevation	−0.081	0.831	−1.681	1.543	0.922	
treatmentF:scale.median_elevation	−0.042	0.774	−1.513	1.516	0.957	
treatmentH:scale.median_elevation	1.255	0.758	−0.165	2.786	0.098	(.)
taxa	66.082	16.965	36.566	98.268	NA	NA
sowing_id	303.383	10298.318	0.000	7.371	NA	NA
units	40.821	3.147	34.767	46.972	NA	NA

variable..LDMC	post.mean	sd	l.95..CI	u.95..CI	pMCMC	sign.
(Intercept)	27.869	485.437	−0.226	37.706	0.954	
treatmentF	0.545	0.422	−0.253	1.384	0.197	
treatmentH	−3.094	0.417	−3.952	−2.304	0.000	***
scale.median_elevation	−1.427	0.480	−2.354	−0.462	0.003	**
treatmentF:scale.median_elevation	0.163	0.413	−0.658	0.948	0.693	
treatmentH:scale.median_elevation	0.047	0.420	−0.771	0.852	0.910	
taxa	23.028	5.620	13.218	34.422	NA	NA
sowing_id	412035.004	18156166.424	0.295	1156.070	NA	NA
units	11.910	0.934	10.259	13.913	NA	NA

variable..LTH	post.mean	sd	l.95..CI	u.95..CI	pMCMC	sign.
(Intercept)	0.274	0.014	0.246	0.301	0.000	***
treatmentF	0.021	0.008	0.006	0.038	0.009	**
treatmentH	−0.006	0.008	−0.023	0.009	0.432	
scale.median_elevation	0.007	0.007	−0.007	0.021	0.334	
treatmentF:scale.median_elevation	−0.006	0.008	−0.022	0.010	0.496	
treatmentH:scale.median_elevation	−0.003	0.008	−0.018	0.013	0.750	
taxa	0.001	0.000	0.001	0.002	NA	NA
units	0.003	0.000	0.002	0.003	NA	NA

variable..LDI.log10	post.mean	sd	l.95..CI	u.95..CI	pMCMC	sign.
(Intercept)	0.332	2.123	−0.155	0.795	0.876	
treatmentF	−0.004	0.006	−0.016	0.007	0.474	
treatmentH	−0.007	0.006	−0.019	0.004	0.226	
scale.median_elevation	0.018	0.011	−0.003	0.038	0.095	(.)
treatmentF:scale.median_elevation	0.008	0.006	−0.004	0.020	0.184	
treatmentH:scale.median_elevation	−0.020	0.006	−0.031	−0.008	0.001	**
taxa	0.022	0.004	0.014	0.030	NA	NA
sowing_id	17.048	526.885	0.000	0.720	NA	NA
units	0.003	0.000	0.002	0.003	NA	NA

variable..RESmT1	post.mean	sd	l.95..CI	u.95..CI	pMCMC	sign.
(Intercept)	68.528	548.888	−18.738	177.826	0.901	
scale.median_elevation	−0.558	0.903	−2.235	1.299	0.537	
taxa	8.562	9.817	0.000	27.894	NA	NA
sowing_id	1340819.223	53537691.609	9.134	32167.614	NA	NA
units	88.918	12.219	66.788	113.352	NA	NA

variable..RESmT2.S1	post.mean	sd	l.95..CI	u.95..CI	pMCMC	sign.
(Intercept)	15.150	2.787	9.428	20.692	0.000	***
scale.median_elevation	4.542	1.561	1.398	7.523	0.004	**
taxa	52.501	39.492	0.001	123.397	NA	NA
units	68.988	25.182	27.489	119.532	NA	NA

variable..RESmT2.S2	post.mean	sd	l.95..CI	u.95..CI	pMCMC	sign.
(Intercept)	59.692	4.311	51.139	68.184	0.000	***
treatmentF	−2.472	1.719	−6.039	0.767	0.151	
scale.median_elevation	0.448	1.653	−3.103	3.412	0.786	
treatmentF:scale.median_elevation	1.235	1.705	−2.131	4.486	0.469	
taxa	151.381	57.271	50.090	261.102	NA	NA
units	126.858	19.322	94.092	166.977	NA	NA

variable..RESpT1	post.mean	sd	l.95..CI	u.95..CI	pMCMC	sign.
(Intercept)	56.544	178.543	3.227	118.390	0.751	
scale.median_elevation	0.749	1.200	−1.534	3.070	0.532	
taxa	54.160	32.138	0.000	110.585	NA	NA
sowing_id	85156.625	1632747.219	1.449	12328.850	NA	NA
units	99.297	18.141	67.356	136.227	NA	NA

variable..RESpT2.S1	post.mean	sd	l.95..CI	u.95..CI	pMCMC	sign.
(Intercept)	18.656	2.860	13.093	24.267	0.000	***
scale.median_elevation	9.009	2.816	2.823	14.081	0.001	**
taxa	6.873	25.193	0.000	35.523	NA	NA
units	333.214	73.367	202.165	472.477	NA	NA

variable..RESpT2.S2.log10	post.mean	sd	l.95..CI	u.95..CI	pMCMC	sign.
(Intercept)	0.955	0.084	0.784	1.115	0.000	***
treatmentH	0.249	0.044	0.165	0.338	0.000	***
scale.median_elevation	−0.101	0.038	−0.174	−0.027	0.008	**
treatmentH:scale.median_elevation	0.075	0.044	−0.012	0.158	0.089	(.)
taxa	0.048	0.022	0.009	0.089	NA	NA
units	0.083	0.012	0.061	0.106	NA	NA

variable..TOL_IGR	post.mean	sd	l.95..CI	u.95..CI	pMCMC	sign.
(Intercept)	0.021	0.025	−0.026	0.069	0.387	
treatmentH	0.003	0.024	−0.044	0.048	0.913	
scale.median_elevation	0.014	0.018	−0.023	0.049	0.437	
treatmentH:scale.median_elevation	0.011	0.024	−0.037	0.057	0.641	
taxa	0.002	0.002	0.000	0.006	NA	NA
units	0.021	0.003	0.017	0.027	NA	NA

variable..TOL_MGR.log10	post.mean	sd	l.95..CI	u.95..CI	pMCMC	sign.
(Intercept)	−0.662	4.228	−1.277	−0.052	0.876	
treatmentH	0.822	0.056	0.721	0.935	0.000	***
scale.median_elevation	0.086	0.067	−0.041	0.221	0.195	
treatmentH:scale.median_elevation	0.124	0.054	0.009	0.221	0.022	*
taxa	0.347	0.105	0.149	0.547	NA	NA
sowing_id	43.666	1957.574	0.000	0.653	NA	NA
units	0.124	0.016	0.095	0.156	NA	NA

variable..TOL_XMID	post.mean	sd	l.95..CI	u.95..CI	pMCMC	sign.
(Intercept)	−0.376	14.313	−0.357	0.411	0.979	
treatmentH	0.018	0.018	−0.016	0.055	0.321	
scale.median_elevation	−0.010	0.016	−0.040	0.022	0.546	
treatmentH:scale.median_elevation	0.050	0.018	0.015	0.085	0.007	**
taxa	0.009	0.005	0.000	0.018	NA	NA
sowing_id	650.521	22176.138	0.000	0.409	NA	NA
units	0.025	0.003	0.020	0.030	NA	NA

variable..TOL_ASYM.log10	post.mean	sd	l.95..CI	u.95..CI	pMCMC	sign.
(Intercept)	−0.417	14.276	−0.416	0.385	0.977	
treatmentH	0.072	0.024	0.024	0.117	0.003	**
scale.median_elevation	0.007	0.022	−0.035	0.051	0.745	
treatmentH:scale.median_elevation	−0.136	0.024	−0.181	−0.090	0.000	***
taxa	0.021	0.010	0.005	0.041	NA	NA
sowing_id	655.381	22184.375	0.000	0.421	NA	NA
units	0.041	0.004	0.033	0.050	NA	NA

Model of trait evolution - A3 (Chapter 1)

AICc values are based on 100 simmMap simulated trees with 2 regimes (high vs. low elevation); mapping was done with 2 different models (ER: equal rate; ARD: all rates different). Mean AICc value was compared. Simulations were conducted on the full tree, while model selection was done on pruned trees. A star (*) indicates thta teh best fitting model was the same independent of the reconstruction regime. Underlines highlight the traits for which OUM was the best model. Further columns provide information on the best model with the lowest mean AICc value, alpha, the phylogenetic half-life (PHL), and the mean AICc value for the Brownian-Motion model (BM_AICc).

Sowing no. 1 (S1)

	Treat.: control (20 °C)	Regime reconstruction : ER				Regime reconstruction : ARD				
	Trait	**BestModel**	**AICc**	**alpha**	**PHL**	**BM_AICc**	**BestModel**	**AICc**	**alpha**	**PHL**	**BM_AICc**
*	ASYM	OUM	624.8	0.2	4.6	644.1	OUM	624.1	0.2	4.3	644.1
	LA	OUM	1038.8	0.3	2.7	1064.5	BMM	1038.4	-	-	1064.5
*	LDI	OUM	124.3	3.0	0.2	196.6	OUM	124.2	3.0	0.2	196.6
*	LDMC	OUM	438.3	29.5	0.1	520.4	OUM	438.3	65.1	0.1	520.4
*	SSIZ	BMM	129.6	-	-	139.7	BMM	128.8	-	-	139.7
*	MGR	OUM	-197.4	60.6	0.0	0.4	OUM	-197.4	99.4	0.0	0.4
*	SLA	OU1	522.0	0.4	1.9	557.9	OU1	522.0	0.4	1.9	557.9
*	TGER	OUM	459.2	307.4	0.0	664.4	OUM	459.2	2079.1	0.0	664.4
*	XMID	OU1	439.2	392.6	0.0	676.9	OU1	439.2	392.6	0.0	676.9

	Treat.: frost (-2 °C, 1 h)	Regime reconstruction : ER				Regime reconstruction : ARD				
	Trait	**BestModel**	**AICc**	**alpha**	**PHL**	**BM_AICc**	**BestModel**	**AICc**	**alpha**	**PHL**	**BM_AICc**
*	ASYM	OUM	487.3	1.9	1.0	520.7	OUM	487.3	0.9	1.2	520.7
*	TOL_ASYM	OU1	-26.2	33.0	0.0	51.5	OU1	-26.2	33.0	0.0	51.5
*	LA	OUM	748.8	2.0	0.8	789.6	OUM	749.1	1.7	0.9	789.6
*	LDI	OU1	93.4	0.3	2.3	118.1	OU1	93.4	0.3	2.3	118.1
*	LDMC	OUM	300.7	0.9	1.4	323.2	OUM	300.4	1.6	1.4	323.2
*	MGR	BMM	11.4	-	-	27.6	BMM	0.8	-	-	27.6
*	TOL_MGR	OU1	91.7	0.2	3.2	108.1	OU1	91.7	0.2	3.2	108.1
*	RESmT1	OU1	410.9	0.4	1.9	437.4	OU1	410.9	0.4	1.9	437.4
*	RESmT2	OUM	404.4	14.8	0.7	430.9	OUM	404.6	12.8	0.8	430.9
*	SLA	OU1	367.6	0.1	4.9	377.5	OU1	367.6	0.1	4.9	377.5
*	XMID	OU1	346.6	2.8	0.3	400.8	OU1	346.6	2.8	0.3	400.8
*	TOL_XMID	OU1	-24.4	0.9	0.7	11.6	OU1	-24.4	0.9	0.7	11.6

	Treat.: heat (+43 °C, 1 h)	Regime reconstruction : ER				Regime reconstruction : ARD				
	Trait	**BestModel**	**AICc**	**alpha**	**PHL**	**BM_AICc**	**BestModel**	**AICc**	**alpha**	**PHL**	**BM_AICc**
*	ASYM	OUM	349.9	0.1	12.6	351.3	OUM	348.9	0.1	11.7	351.3
*	TOL_ASYM	BMM	126.7	-	-	131.2	BMM	122.7	-	-	131.2
*	LA	BMM	547.5	-	-	548.9	BMM	546.2	-	-	548.9
*	LDI	OUM	66.7	0.1	7.2	69.6	OUM	65.6	0.1	6.7	69.6
*	LDMC	OU1	264.3	3.1	0.2	288.7	OU1	264.3	3.1	0.2	288.7
*	MGR	OU1	-57.3	1.3	0.5	-4.5	OU1	-57.3	1.3	0.5	-4.5
*	TOL_MGR	OU1	52.8	2.8	0.3	116.6	OU1	52.8	2.8	0.3	116.6
	RESpT1	OUM	301.4	0.1	5.5	303.9	OU1	302.5	0.1	4.8	303.9
*	RESpT2	OUM	329.2	19.5	0.3	362.6	OUM	329.2	25.2	0.3	362.6
*	SLA	OU1	288.7	2.5	0.3	336.1	OU1	288.7	2.5	0.3	336.1
*	XMID	OUM	244.1	86.0	0.1	285.4	OUM	244.1	80.0	0.1	285.4

* TOL_XMID	OU1	-10.1	19.1	0.0	43.9	OU1	-10.1	19.1	0.0	43.9

Sowing no. 2 (S2)

Treat.: control (20 °C)		Regime reconstruction : ER				Regime reconstruction : ARD				
Trait	**BestModel**	**AICc**	**alpha**	**PHL**	**BM_AICc**	**BestModel**	**AICc**	**alpha**	**PHL**	**BM_AICc**
* ASYM	OU1	678.6	0.1	6.9	691.3	OU1	678.6	0.1	6.9	691.3
* IGR	OUM	-247.3	206.9	0.0	-157.1	OUM	-247.3	148.9	0.0	-157.1
* LA	BMM	1082.9	-	-	1092.3	BMM	1082.4	-	-	1092.3
* LDI	OU1	90.8	0.1	8.7	102.2	OU1	90.8	0.1	8.7	102.2
* LDMC	OUM	448.6	0.5	1.3	494.1	OUM	448.7	0.5	1.3	494.1
* SSIZ	OU1	167.6	0.1	6.0	179.0	OU1	167.6	0.1	6.0	179.0
* LTH	OUM	-220.0	0.3	2.4	-186.3	OUM	-219.4	0.3	2.4	-186.3
* MGR	OUM	-266.3	61.5	0.1	-162.7	OUM	-266.3	22.0	0.1	-162.7
* NLEA	OU1	593.7	0.1	7.1	601.5	OU1	593.7	0.1	7.1	601.5
* RESmT1	OU1	531.1	0.4	1.6	577.7	OU1	531.1	0.4	1.6	577.7
* RESmT2	OU1	632.0	1.6	0.4	693.3	OU1	632.0	1.6	0.4	693.3
* RESpT1	OU1	583.6	3.3	0.2	695.0	OU1	583.6	3.3	0.2	695.0
* RESpT2	OUM	526.1	23.8	0.4	591.7	OUM	526.0	9.9	0.4	591.7
* SLA	OU1	542.2	0.5	1.5	592.1	OU1	542.2	0.5	1.5	592.1
* TGER	OUM	305.2	0.4	1.7	342.0	OUM	304.9	0.4	1.7	342.0
* XMID	OU1	416.9	1.0	0.7	480.0	OU1	416.9	1.0	0.7	480.0

Treat.: frost (-2 °C, 1 h)		Regime reconstruction : ER				Regime reconstruction : ARD				
Trait	**BestModel**	**AICc**	**alpha**	**PHL**	**BM_AICc**	**BestModel**	**AICc**	**alpha**	**PHL**	**BM_AICc**
* ASYM	OUM	636.1	0.2	4.5	655.5	OUM	635.5	0.2	4.3	655.5
* TOL_ASYM	OUM	-15.2	125.1	0.0	110.9	OUM	-15.2	77.1	0.0	110.9
* IGR	OU1	-253.8	28.2	0.0	-139.3	OU1	-253.8	28.2	0.0	-139.3
* TOL_IGR	OU1	-95.4	2.6	0.3	-15.4	OU1	-95.4	2.6	0.3	-15.4
* LA	OUM	1052.3	0.2	2.8	1079.5	OUM	1052.1	0.3	2.8	1079.5
* LDI	OU1	121.4	0.1	8.2	131.9	OU1	121.4	0.1	8.2	131.9
* LDMC	OUM	416.6	1.7	0.6	470.7	OUM	416.5	1.2	0.6	470.7
* LTH	OU1	-207.5	8.5	0.1	-118.2	OU1	-207.5	8.5	0.1	-118.2
* MGR	OU1	-151.5	23.7	0.0	-54.1	OU1	-151.5	23.7	0.0	-54.1
* TOL_MGR	OU1	86.1	6.2	0.1	200.8	OU1	86.1	6.2	0.1	200.8
* NLEA	OU1	550.0	0.2	3.7	570.9	OU1	550.0	0.2	3.7	570.9
* RESmT2	OU1	602.1	0.7	0.9	642.4	OU1	602.1	0.7	0.9	642.4
* SLA	OU1	478.4	1.0	0.7	548.7	OU1	478.4	1.0	0.7	548.7
* XMID	OU1	390.8	15.1	0.0	468.3	OU1	390.8	15.1	0.0	468.3
* TOL_XMID	OU1	-60.4	25.7	0.0	37.8	OU1	-60.4	25.7	0.0	37.8

Treat.: heat (+40 °C, 1 h)		Regime reconstruction : ER				Regime reconstruction : ARD				
Trait	**BestModel**	**AICc**	**alpha**	**PHL**	**BM_AICc**	**BestModel**	**AICc**	**alpha**	**PHL**	**BM_AICc**
* ASYM	OUM	692.1	0.3	2.7	725.2	OUM	689.9	0.3	2.7	725.2
* TOL_ASYM	OUM	232.2	0.9	0.8	308.6	OUM	232.1	0.9	0.8	308.6
* IGR	OU1	-192.7	25.4	0.0	-105.3	OU1	-192.7	25.4	0.0	-105.3
* TOL_IGR	OU1	-49.2	22.2	0.0	80.2	OU1	-49.2	22.2	0.0	80.2
* LA	OUM	1116.1	1.0	1.5	1151.2	OUM	1115.4	0.4	1.8	1151.2
* LDI	OUM	124.0	0.1	5.1	142.7	OUM	123.8	0.1	5.0	142.7

* LDMC	OUM	417.9	0.7	1.6	453.1	OUM	418.1	0.5	1.6	453.1
* LTH	OU1	-218.0	21.4	0.0	-132.3	OU1	-218.0	21.4	0.0	-132.3
* MGR	OU1	97.7	0.7	1.0	150.4	OU1	97.7	0.7	1.0	150.4
* TOL_MGR	OUM	319.2	0.8	0.8	376.7	OUM	319.2	0.8	0.8	376.7
* NLEA	OU1	571.5	0.1	6.0	582.3	OU1	571.5	0.1	6.0	582.3
* RESpT2	OU1	619.7	9.1	0.1	743.0	OU1	619.7	9.1	0.1	743.0
* SLA	OUM	543.8	1.4	0.5	621.6	OUM	543.8	1.4	0.5	621.6
* XMID	OUM	388.0	53.0	0.2	447.3	OUM	388.1	67.2	0.2	447.3
* TOL_XMID	OUM	-42.1	0.4	1.7	-8.5	OUM	-41.7	0.4	1.8	-8.5

Sowing N. 1 (S1) - Stochastic map : ER - Treatment : C

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
ASYM	OUM	-308.1153	624.2305	624.8459	4	67.14908	37.80196	67.98115	167.41468	NA	NA	0.1548032	4.557993
ASYM	OU1	-311.2708	628.5416	628.9053	3	60.98784	NA	NA	138.6355	NA	NA	0.1033539	6.706542
ASYM	BM	-319.9669	643.9339	644.113	2	60.96	NA	NA	76.82928	NA	NA	NA	NA
ASYM	BMM	-319.8319	645.6638	646.0275	3	61.03909	NA	NA	NA	81.35153	75.25119	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
LA	OUM	-515.1011	1038.202	1038.818	4	636.7751	167.8869	650.9847	97130.73	NA	NA	0.2722521	2.714411
LA	OU1	-518.5204	1043.041	1043.404	3	534.8684	NA	NA	66369.23	NA	NA	0.1484084	4.67054
LA	BMM	-519.2059	1044.412	1044.775	3	474.2417	NA	NA	NA	3854.052	40149.82	NA	NA
LA	BM	-530.1792	1064.358	1064.537	2	537.5796	NA	NA	31183.65	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
LDI	OUM	-57.82457	123.6491	124.2645	4	2.316795	2.017052	2.326033	1.9157941	NA	NA	3.03674	0.2431353
LDI	OU1	-59.89393	125.7879	126.1515	3	2.222585	NA	NA	2.1041901	NA	NA	3.149942	0.2200508
LDI	BMM	-76.62102	159.242	159.6057	3	2.270865	NA	NA	NA	0.295579	0.03700794	NA	NA
LDI	BM	-96.23063	196.4613	196.6404	2	2.24223	NA	NA	0.1286217	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
LDMC	OUM	-214.852	437.704	438.3194	4	22.10962	18.3597	22.22409	1614.97931	NA	NA	29.479807	0.1191799
LDMC	OU1	-218.6249	443.2499	443.6135	3	20.93287	NA	NA	350.25629	NA	NA	5.693101	0.1217521
LDMC	BMM	-256.8012	519.6023	519.966	3	21.09351	NA	NA	NA	18.5201	10.81222	NA	NA
LDMC	BM	-258.0959	520.1918	520.3709	2	20.90955	NA	NA	13.11612	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
SSIZ	BMM	-61.63601	129.272	129.6357	3	1.23215	NA	NA	NA	0.1213319	0.03151353	NA	NA
SSIZ	OU1	-64.59303	135.1861	135.5497	3	1.150089	NA	NA	0.09204459	NA	NA	0.06417086	10.80159
SSIZ	OUM	-64.32863	136.6573	137.2726	4	1.16448	1.029021	1.174652	0.09115589	NA	NA	0.06387564	10.86252
SSIZ	BM	-67.76657	139.5331	139.7122	2	1.2283	NA	NA	0.05703222	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
MGR	OUM	103.006166	-198.0123322	-197.3969476	4	0.1669773	0.139758	0.1678216	0.374255069	NA	NA	60.62422	0.01148402
MGR	OU1	101.116288	-196.2325754	-195.868939	3	0.1584527	NA	NA	3.870207972	NA	NA	594.14114	0.001166637
MGR	BMM	40.022436	-74.0448724	-73.6812361	3	0.1619489	NA	NA	NA	0.01850687	0.000931032	NA	NA
MGR	BM	1.901558	0.1968846	0.3759891	2	0.1580591	NA	NA	0.007792006	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
SLA	OU1	-257.8343	521.6685	522.0322	3	24.9425	NA	NA	78.88103	NA	NA	0.357944	1.936468
SLA	OUM	-257.6421	523.2843	523.8997	4	24.55904	26.06718	24.54207	79.46911	NA	NA	0.3633297	1.910829
SLA	BMM	-274.9346	555.8692	556.2328	3	25.10843	NA	NA	NA	34.09316	17.37964	NA	NA
SLA	BM	-276.8835	557.767	557.9461	2	25.09703	NA	NA	22.4352	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
TGER	OUM	-225.2936	458.5872	459.2026	4	11.22178	15.49095	11.08986	22478.0846	NA	NA	307.37467	0.002717366
TGER	OU1	-229.2278	464.4557	464.8193	3	12.58498	NA	NA	6556.6565	NA	NA	80.12489	0.008650834
TGER	BMM	-292.4851	590.9703	591.3339	3	12.79728	NA	NA	NA	245.0379	12.49491	NA	NA
TGER	BM	-330.0898	664.1796	664.3587	2	13.90101	NA	NA	102.5972	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
XMID	OU1	-216.4246	438.8492	439.2128	3	-33.28944	NA	NA	22282.4584	NA	NA	392.5714	0.001765659
XMID	OUM	-216.2816	440.5633	441.1787	4	-33.06585	-33.76025	-33.04362	22943.7812	NA	NA	405.8715	0.00191308
XMID	BMM	-281.0021	568.0043	568.3679	3	-32.57505	NA	NA	NA	298.9032	6.279554	NA	NA
XMID	BM	-336.3835	676.7669	676.946	2	-32.96187	NA	NA	122.8089	NA	NA	NA	NA

Sowing N. 1 (S1) - Stochastic map : ARD - Treatment : C

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
ASYM	OUM	-307.7495	623.4991	624.1144	4	52.87079	41.09854	70.79343	172.12243	NA	NA	0.1627679	4.342452
ASYM	OU1	-311.2708	628.5416	628.9053	3	60.98784	NA	NA	138.6355	NA	NA	0.1033539	6.706542
ASYM	BM	-319.9669	643.9339	644.113	2	60.96	NA	NA	76.82928	NA	NA	NA	NA
ASYM	BMM	-319.6215	645.2429	645.6065	3	60.47765	NA	NA	NA	71.42045	80.81304	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
LA	BMM	-515.996	1037.992	1038.356	3	417.0547	NA	NA	NA	3844.172	45031.35	NA	NA
LA	OUM	-514.9435	1037.887	1038.502	4	388.0613	201.6222	673.9068	99655.19	NA	NA	0.2817699	2.674109
LA	OU1	-518.5204	1043.041	1043.404	3	534.8684	NA	NA	66369.23	NA	NA	0.1484084	4.67054
LA	BM	-530.1792	1064.358	1064.537	2	537.5796	NA	NA	31183.65	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
LDI	OUM	-57.81199	123.624	124.2394	4	2.138039	2.017985	2.328055	1.9015941	NA	NA	3.012618	0.2491246
LDI	OU1	-59.89393	125.7879	126.1515	3	2.222585	NA	NA	2.1041901	NA	NA	3.149942	0.2200508
LDI	BMM	-81.6537	169.3074	169.671	3	2.296986	NA	NA	NA	0.2396391	0.04061928	NA	NA
LDI	BM	-96.23063	196.4613	196.6404	2	2.24223	NA	NA	0.1286217	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
LDMC	OUM	-214.8389	437.6778	438.2932	4	19.8852	18.37204	22.23748	3565.20421	NA	NA	65.149999	0.1104205
LDMC	OU1	-218.6249	443.2499	443.6135	3	20.93287	NA	NA	350.25629	NA	NA	5.693101	0.1217521
LDMC	BM	-258.0959	520.1918	520.3709	2	20.90955	NA	NA	13.11612	NA	NA	NA	NA
LDMC	BMM	-257.6685	521.337	521.7006	3	21.00023	NA	NA	NA	15.31463	11.93335	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
SSIZ	BMM	-61.23663	128.4733	128.8369	3	1.238958	NA	NA	NA	0.1110744	0.02688366	NA	NA
SSIZ	OU1	-64.59303	135.1861	135.5497	3	1.150089	NA	NA	0.09204459	NA	NA	0.06417086	10.80159
SSIZ	OUM	-64.2967	136.5934	137.2088	4	1.135349	1.046663	1.208829	0.09129282	NA	NA	0.06419929	10.80777
SSIZ	BM	-67.76657	139.5331	139.7122	2	1.2283	NA	NA	0.05703222	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
MGR	OUM	102.997542	-197.9950834	-197.3796988	4	0.1507423	0.1398464	0.1678061	0.613652359	NA	NA	99.35179	0.011116286
MGR	OU1	101.116288	-196.2325754	-195.868939	3	0.1584527	NA	NA	3.870207972	NA	NA	594.14114	0.001166637
MGR	BMM	30.732562	-55.4651238	-55.1014874	3	0.162579	NA	NA	NA	0.01480445	0.001102323	NA	NA
MGR	BM	1.901558	0.1968846	0.3759891	2	0.1580591	NA	NA	0.007792006	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
SLA	OU1	-257.8343	521.6685	522.0322	3	24.9425	NA	NA	78.88103	NA	NA	0.357944	1.936468
SLA	OUM	-257.6615	523.323	523.9384	4	25.44241	25.99576	24.48755	79.484	NA	NA	0.363157	1.910267
SLA	BM	-276.8835	557.767	557.9461	2	25.09703	NA	NA	22.4352	NA	NA	NA	NA
SLA	BMM	-276.0143	558.0286	558.3923	3	25.06799	NA	NA	NA	28.43345	18.94921	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
TGER	OUM	-225.2939	458.5878	459.2032	4	13.77361	15.48933	11.08927	152058.8747	NA	NA	2079.13	0.002583798
TGER	OU1	-229.2278	464.4557	464.8193	3	12.58498	NA	NA	6556.6565	NA	NA	80.12489	0.008650834
TGER	BMM	-301.5679	609.1357	609.4994	3	13.47238	NA	NA	NA	195.7228	14.66204	NA	NA
TGER	BM	-330.0898	664.1796	664.3587	2	13.90101	NA	NA	102.5972	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
XMID	OU1	-216.4246	438.8492	439.2128	3	-33.28944	NA	NA	22282.4584	NA	NA	392.5714	0.001765659
XMID	OUM	-216.2815	440.563	441.1784	4	-33.48285	-33.76124	-33.0432	75018.5503	NA	NA	1327.0441	0.001987878
XMID	BMM	-293.1623	592.3245	592.6881	3	-32.68421	NA	NA	NA	235.9258	7.371339	NA	NA
XMID	BM	-336.3835	676.7669	676.946	2	-32.96187	NA	NA	122.8089	NA	NA	NA	NA

Sowing N. 1 (S1) - Stochastic map : ER - Treatment : F

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
ASYM	OUM	-239.2184	486.4368	487.2701	4	58.89079	36.48469	59.53879	1890.1099	NA	NA	1.861157	1.013481
ASYM	OU1	-242.8703	491.7407	492.2305	3	52.75304	NA	NA	386.4173	NA	NA	0.31188	2.222481
ASYM	BMM	-255.4667	516.9335	517.4233	3	51.37024	NA	NA	NA	43.21401	137.9372	NA	NA
ASYM	BM	-258.2513	520.5027	520.7427	2	52.90055	NA	NA	115.1571	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
TOL_ASYM	OU1	16.33681	-26.67362	-26.18382	3	-0.12242124	NA	NA	2.08885286	NA	NA	33.04209	0.02097771
TOL_ASYM	OUM	16.34184	-24.68368	-23.85034	4	-0.1236125	-0.1201186	-0.1235775	2.31320217	NA	NA	36.59671	0.02206971
TOL_ASYM	BM	-23.65098	51.30197	51.54197	2	-0.06766053	NA	NA	0.01646453	NA	NA	NA	NA
TOL_ASYM	BMM	-22.97214	51.94427	52.43407	3	-0.06780168	NA	NA	NA	0.01139544	0.0182369	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life

LA	OUM	-369.9994	747.9988	748.8321	4	448.576	226.1251	455.5068	279463.25	NA	NA	2.0082507	0.7886924
LA	OU1	-372.8594	751.7188	752.2086	3	382.4924	NA	NA	75786.62	NA	NA	0.4708948	1.4719787
LA	BM	-392.7017	789.4034	789.6434	2	369.7714	NA	NA	18396.14	NA	NA	NA	NA
LA	BMM	-392.3032	790.6065	791.0963	3	363.6387	NA	NA	NA	14144.64	20018.24	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
LDI	OU1	-43.45716	92.91431	93.40411	3	2.17475	NA	NA	0.20356243	NA	NA	0.3036673	2.282588
LDI	OUM	-42.98088	93.96176	94.79509	4	2.219236	2.052463	2.224435	0.20537916	NA	NA	0.3126536	2.274332
LDI	BMM	-55.75431	117.50862	117.99842	3	2.175367	NA	NA	NA	0.03295174	0.06651649	NA	NA
LDI	BM	-56.94656	117.89313	118.13313	2	2.180739	NA	NA	0.05783798	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
LDMC	OUM	-145.9211	299.8422	300.6755	4	23.02696	17.92286	23.17663	28.290205	NA	NA	0.9381903	1.436174
LDMC	OU1	-151.183	308.366	308.8558	3	21.58047	NA	NA	7.39598	NA	NA	0.1744742	3.972779
LDMC	BM	-159.4962	322.9924	323.2324	2	21.00466	NA	NA	2.772328	NA	NA	NA	NA
LDMC	BMM	-158.8897	323.7795	324.2693	3	20.80386	NA	NA	NA	1.908503	3.076261	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
MGR	BMM	-2.449911	10.89982	11.38962	3	0.1587283	NA	NA	NA	0.001765089	0.01262476	NA	NA
MGR	OU1	-5.546978	17.09396	17.58375	3	0.1904859	NA	NA	0.02597778	NA	NA	0.1433165	4.836479
MGR	OUM	-5.061546	18.12309	18.95643	4	0.2213246	0.0883067	0.2256627	0.0271918	NA	NA	0.1555592	4.459928
MGR	BM	-11.688493	27.37699	27.61699	2	0.1716436	NA	NA	0.01048341	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
TOL_MGR	OU1	-42.60716	91.21432	91.70412	3	0.1357105	NA	NA	0.14521097	NA	NA	0.213369	3.248584
TOL_MGR	OUM	-42.47063	92.94126	93.77459	4	0.1301834	0.1611568	0.1293418	0.14200094	NA	NA	0.2089729	3.324514
TOL_MGR	BM	-51.94141	107.88282	108.12282	2	0.2228726	NA	NA	0.04788354	NA	NA	NA	NA
TOL_MGR	BMM	-51.2173	108.4346	108.9244	3	0.217788	NA	NA	NA	0.06534799	0.04143556	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
RESmT1	OU1	-202.1873	410.3746	410.8644	3	57.95591	NA	NA	95.96605	NA	NA	0.365559	1.89613
RESmT1	OUM	-202.1212	412.2424	413.0757	4	57.79705	58.43941	57.77248	93.58889	NA	NA	0.3564917	1.948109
RESmT1	BM	-216.5873	437.1745	437.4145	2	57.93108	NA	NA	23.90453	NA	NA	NA	NA
RESmT1	BMM	-216.5184	439.0367	439.5265	3	57.9341	NA	NA	NA	25.15758	23.58329	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
RESmT2	OUM	-197.794	403.5879	404.4213	4	13.00361	19.87702	12.80822	3038.40472	NA	NA	14.8459716	0.7445027
RESmT2	OU1	-199.4686	404.9371	405.4269	3	14.89936	NA	NA	96.04705	NA	NA	0.4097406	1.6916733
RESmT2	BMM	-211.8776	429.7552	430.245	3	15.70249	NA	NA	NA	34.21408	16.30348	NA	NA
RESmT2	BM	-213.3224	430.6447	430.8847	2	15.70206	NA	NA	21.1336	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
SLA	OU1	-180.5631	367.1263	367.6161	3	22.63347	NA	NA	19.051824	NA	NA	0.1420776	4.878652
SLA	OUM	-180.2699	368.5397	369.373	4	22.16371	24.17773	22.14391	19.342559	NA	NA	0.1469943	4.727909
SLA	BM	-186.6074	377.2149	377.4549	2	22.87405	NA	NA	7.711811	NA	NA	NA	NA
SLA	BMM	-186.5766	379.1532	379.643	3	22.84966	NA	NA	NA	7.988746	7.629708	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
XMID	OU1	-170.0451	346.0901	346.5799	3	-32.32439	NA	NA	198.85227	NA	NA	2.764707	0.2507127
XMID	OUM	-169.2627	346.5255	347.3588	4	-31.63291	-33.80067	-31.56212	1740.94112	NA	NA	24.928256	0.2455432
XMID	BM	-198.3012	400.6024	400.8424	2	-33.14712	NA	NA	11.98945	NA	NA	NA	NA
XMID	BMM	-197.3262	400.6525	401.1423	3	-32.99478	NA	NA	NA	17.0879	10.0249	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
TOL_XMID	OU1	15.461379	-24.92276	-24.43296	3	0.023585149	NA	NA	0.062974623	NA	NA	0.9401029	0.7373099
TOL_XMID	OUM	15.497497	-22.99499	-22.16166	4	0.024029532	0.02274583	0.02392476	0.061606423	NA	NA	0.9200796	0.7552731
TOL_XMID	BM	-3.684725	11.36945	11.60945	2	-0.004928717	NA	NA	0.007750558	NA	NA	NA	NA
TOL_XMID	BMM	-3.606466	13.21293	13.70273	3	-0.004301097	NA	NA	NA	0.007749749	0.007800165	NA	NA

Sowing N. 1 (S1) - Stochastic map : ARD - Treatment : F

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
ASYM	OUM	-239.2416	486.4832	487.3165	4	46.0728	37.12696	59.82611	907.1254	NA	NA	0.8934355	1.160177
ASYM	OU1	-242.8703	491.7407	492.2305	3	52.75304	NA	NA	386.4173	NA	NA	0.31188	2.222481
ASYM	BMM	-253.6746	513.3492	513.839	3	49.8597	NA	NA	NA	38.71474	152.7001	NA	NA
ASYM	BM	-258.2513	520.5027	520.7427	2	52.90055	NA	NA	115.1571	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
TOL_ASYM	OU1	16.33681	-26.67362	-26.18382	3	-0.12242124	NA	NA	2.08885286	NA	NA	33.04209	0.02097771
TOL_ASYM	OUM	16.34203	-24.68405	-23.85072	4	-0.12131526	-0.1198982	-0.1236964	2.69498539	NA	NA	42.63929	0.02178594
TOL_ASYM	BMM	-21.55413	49.10827	49.59806	3	-0.06792046	NA	NA	NA	0.009146489	0.02015783	NA	NA
TOL_ASYM	BM	-23.65098	51.30197	51.54197	2	-0.06766053	NA	NA	0.01646453	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
LA	OUM	-370.1189	748.2377	749.0711	4	321.3335	234.7846	455.5627	243869.59	NA	NA	1.7449661	0.8837824
LA	OU1	-372.8594	751.7188	752.2086	3	382.4924	NA	NA	75786.62	NA	NA	0.4708948	1.4719787
LA	BMM	-391.2913	788.5827	789.0725	3	357.7548	NA	NA	NA	11604.01	22232.07	NA	NA
LA	BM	-392.7017	789.4034	789.6434	2	369.7714	NA	NA	18396.14	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
LDI	OU1	-43.45716	92.91431	93.40411	3	2.17475	NA	NA	0.20356243	NA	NA	0.3036673	2.282588
LDI	OUM	-42.9547	93.90939	94.74273	4	2.116704	2.046938	2.234582	0.20597367	NA	NA	0.3142276	2.244154
LDI	BMM	-54.29699	114.59398	115.08378	3	2.157876	NA	NA	NA	0.02747852	0.07365124	NA	NA
LDI	BM	-56.94656	117.89313	118.13313	2	2.180739	NA	NA	0.05783798	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
LDMC	OUM	-145.8061	299.6121	300.4454	4	20.14666	18.11344	23.30109	46.79248	NA	NA	1.5689893	1.445965
LDMC	OU1	-151.183	308.366	308.8558	3	21.58047	NA	NA	7.39598	NA	NA	0.1744742	3.972779
LDMC	BMM	-158.0701	322.1402	322.63	3	20.60998	NA	NA	NA	1.710833	3.344485	NA	NA
LDMC	BM	-159.4962	322.9924	323.2324	2	21.00466	NA	NA	2.772328	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
MGR	BMM	2.857958	0.2840848	0.7738807	3	0.1437242	NA	NA	NA	0.001458796	0.01394168	NA	NA
MGR	OU1	-5.546978	17.0939557	17.5837516	3	0.1904859	NA	NA	0.02597778	NA	NA	0.1433165	4.836479
MGR	OUM	-4.960632	17.9212632	18.7545966	4	0.149938	0.1019977	0.2413214	0.02717168	NA	NA	0.1561563	4.448027
MGR	BM	-11.688493	27.3769866	27.6169866	2	0.1716436	NA	NA	0.01048341	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
TOL_MGR	OU1	-42.60716	91.21432	91.70412	3	0.1357105	NA	NA	0.14521097	NA	NA	0.213369	3.248584
TOL_MGR	OUM	-42.48067	92.96133	93.79467	4	0.1710396	0.167286	0.1179828	0.14241083	NA	NA	0.2096577	3.309914
TOL_MGR	BM	-51.94141	107.88282	108.12282	2	0.2228726	NA	NA	0.04788354	NA	NA	NA	NA
TOL_MGR	BMM	-51.71613	109.43227	109.92206	3	0.2201842	NA	NA	NA	0.05429043	0.04472683	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
RESmT1	OU1	-202.1873	410.3746	410.8644	3	57.95591	NA	NA	95.96605	NA	NA	0.365559	1.89613
RESmT1	OUM	-202.1065	412.213	413.0464	4	58.17099	58.21637	57.84734	93.27375	NA	NA	0.355352	1.956342
RESmT1	BM	-216.5873	437.1745	437.4145	2	57.93108	NA	NA	23.90453	NA	NA	NA	NA
RESmT1	BMM	-216.2771	438.5542	439.044	3	57.95326	NA	NA	NA	20.66135	25.99686	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
RESmT2	OUM	-197.8588	403.7177	404.551	4	16.97884	19.66869	12.74269	2618.84213	NA	NA	12.7908012	0.7884375
RESmT2	OU1	-199.4686	404.9371	405.4269	3	14.89936	NA	NA	96.04705	NA	NA	0.4097406	1.6916733
RESmT2	BM	-213.3224	430.6447	430.8847	2	15.70206	NA	NA	21.1336	NA	NA	NA	NA
RESmT2	BMM	-212.7323	431.4647	431.9545	3	15.61723	NA	NA	NA	27.14696	18.03882	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
SLA	OU1	-180.5631	367.1263	367.6161	3	22.63347	NA	NA	19.051824	NA	NA	0.1420776	4.878652
SLA	OUM	-180.2008	368.4015	369.2348	4	23.39249	24.17245	21.73459	19.305466	NA	NA	0.1470834	4.722668
SLA	BM	-186.6074	377.2149	377.4549	2	22.87405	NA	NA	7.711811	NA	NA	NA	NA
SLA	BMM	-186.4856	378.9711	379.4609	3	22.87282	NA	NA	NA	7.163177	8.073661	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
XMID	OU1	-170.0451	346.0901	346.5799	3	-32.32439	NA	NA	198.85227	NA	NA	2.764707	0.2507127
XMID	OUM	-169.2454	346.4908	347.3241	4	-32.95865	-33.81859	-31.54368	3442.14025	NA	NA	49.285854	0.2687753
XMID	BM	-198.3012	400.6024	400.8424	2	-33.14712	NA	NA	11.98945	NA	NA	NA	NA

XMID	BMM	-198.0365	402.073	402.5628	3	-33.07467	NA	NA	NA	13.79295	11.10497	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
TOL_XMID	OU1	15.461379	-24.92276	-24.43296	3	0.023585149	NA	NA	0.062974623	NA	NA	0.9401029	0.7373099
TOL_XMID	OUM	15.505976	-23.01195	-22.17862	4	0.020926546	0.02295832	0.0237423	0.061353156	NA	NA	0.9163037	0.7628738
TOL_XMID	BM	-3.684725	11.36945	11.60945	2	-0.004928717	NA	NA	0.007750558	NA	NA	NA	NA
TOL_XMID	BMM	-3.261131	12.52226	13.01206	3	-0.004209389	NA	NA	NA	0.006368716	0.008591619	NA	NA

Sowing N. 1 (S1) - Stochastic map : ER - Treatment : H

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
ASYM	OUM	-170.3254	348.6507	349.8629	4	59.7129	-2.765647	61.7985	80.5982	NA	NA	0.05622795	12.6065
ASYM	BM	-173.4666	350.9331	351.276	2	51.40392	NA	NA	53.01059	NA	NA	NA	NA
ASYM	OU1	-172.6938	351.3877	352.0935	3	51.86213	NA	NA	71.83887	NA	NA	0.03141865	22.06165
ASYM	BMM	-172.8948	351.7897	352.4955	3	49.56853	NA	NA	NA	32.63013	60.18685	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
TOL_ASYM	BMM	-60.00893	126.0179	126.7237	3	0.009853688	NA	NA	NA	0.04062193	0.1958981	NA	NA
TOL_ASYM	OU1	-60.34494	126.6899	127.3958	3	0.218192775	NA	NA	0.3021266	NA	NA	0.07972246	8.694504
TOL_ASYM	OUM	-59.49726	126.9945	128.2066	4	0.43334477	-0.8446074	0.4750724	0.316448	NA	NA	0.09136454	7.593302
TOL_ASYM	BM	-63.41573	130.8315	131.1743	2	0.123295474	NA	NA	0.1617576	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
LA	BMM	-270.3983	546.7965	547.5024	3	361.4774	NA	NA	NA	3378.503	11716.81	NA	NA
LA	BM	-272.2662	548.5323	548.8752	2	399.5467	NA	NA	9609.155	NA	NA	NA	NA
LA	OUM	-270.3654	548.7309	549.943	4	485.5153	-306.9211	514.8448	13849.608	NA	NA	0.04354595	16.08752
LA	OU1	-271.8144	549.6288	550.3347	3	406.8153	NA	NA	12986.186	NA	NA	0.02951067	23.48802

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
LDI	OUM	-28.72512	65.45024	66.66236	4	2.201635	1.474972	2.225625	0.0656209	NA	NA	0.09770159	7.199923
LDI	OU1	-30.07237	66.14474	66.85063	3	2.069008	NA	NA	0.05567876	NA	NA	0.06794279	10.201924
LDI	BM	-32.61289	69.22577	69.56863	2	2.054505	NA	NA	0.03197314	NA	NA	NA	NA
LDI	BMM	-32.22736	70.45472	71.1606	3	2.034613	NA	NA	NA	0.02306664	0.03521752	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
LDMC	OU1	-128.7909	263.5818	264.2877	3	18.14981	NA	NA	319.72898	NA	NA	3.107117	0.2230837
LDMC	OUM	-127.919	263.8381	265.0502	4	19.08171	15.7465	19.18578	1237.47911	NA	NA	12.543796	0.2344454
LDMC	BM	-142.185	288.3701	288.7129	2	18.86255	NA	NA	10.21744	NA	NA	NA	NA
LDMC	BMM	-141.9438	289.8876	290.5935	3	18.93077	NA	NA	NA	12.63835	9.408878	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
MGR	OU1	32.008092	-58.016184	-57.3103	3	0.205853	NA	NA	0.02915668	NA	NA	1.334165	0.5195362
MGR	OUM	32.585183	-57.170366	-55.95824	4	0.1948509	0.2359053	0.1936311	0.034450666	NA	NA	1.628314	0.4301315
MGR	BMM	21.29888	-36.597761	-35.89188	3	0.1956663	NA	NA	NA	0.01172273	0.000792878	NA	NA
MGR	BM	4.405274	-4.810547	-4.46769	2	0.2050837	NA	NA	0.004556578	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
TOL_MGR	OU1	-23.06859	52.13718	52.84306	3	-0.11991564	NA	NA	1.0884197	NA	NA	2.758722	0.2512566
TOL_MGR	OUM	-22.56885	53.1377	54.34982	4	-0.07345231	-0.2333571	-0.06853437	20.2589315	NA	NA	52.699622	0.1144871
TOL_MGR	BM	-56.1534	116.3068	116.64966	2	-0.13834225	NA	NA	0.1103736	NA	NA	NA	NA
TOL_MGR	BMM	-55.82277	117.64553	118.35141	3	-0.14614806	NA	NA	NA	0.084722	0.1199682	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
RESpT1	OUM	-146.0897	300.1794	301.3915	4	59.22653	44.89798	59.54983	42.83537	NA	NA	0.1413952	5.510934
RESpT1	OU1	-147.8904	301.7808	302.4867	3	56.73243	NA	NA	47.42497	NA	NA	0.1457837	4.754628
RESpT1	BM	-149.7698	303.5396	303.8825	2	55.61755	NA	NA	15.23042	NA	NA	NA	NA
RESpT1	BMM	-149.2993	304.5986	305.3045	3	56.6281	NA	NA	NA	22.50062	12.96203	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
RESpT2	OUM	-159.9707	327.9414	329.1535	4	12.13941	30.96996	11.58253	10491.98602	NA	NA	19.525175	0.3146234
RESpT2	OU1	-164.5282	335.0563	335.7622	3	17.33239	NA	NA	1059.38613	NA	NA	1.563466	0.44334
RESpT2	BMM	-170.9599	347.9197	348.6256	3	14.87048	NA	NA	NA	205.4222	24.24582	NA	NA
RESpT2	BM	-179.1144	362.2288	362.5716	2	17.77633	NA	NA	71.36064	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
SLA	OU1	-141.0174	288.0348	288.7406	3	27.21867	NA	NA	490.62049	NA	NA	2.503313	0.276892
SLA	OUM	-141.0036	290.0072	291.2193	4	27.09391	27.50997	27.09161	497.47673	NA	NA	2.540203	0.2736016
SLA	BMM	-159.8145	325.6289	326.3348	3	26.07306	NA	NA	NA	76.46032	16.44011	NA	NA
SLA	BM	-165.8988	335.7977	336.1405	2	26.18633	NA	NA	35.59448	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
XMID	OUM	-117.4504	242.9008	244.1129	4	-30.12116	-27.11235	-30.21329	4875.630924	NA	NA	85.998258	0.05271769
XMID	OU1	-118.7241	243.4481	244.154	3	-29.31193	NA	NA	559.94685	NA	NA	9.244741	0.07497746
XMID	BMM	-139.2009	284.4018	285.1077	3	-29.66555	NA	NA	NA	14.95849	7.165101	NA	NA
XMID	BM	-140.5041	285.0082	285.351	2	-29.49912	NA	NA	9.352322	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
TOL_XMID	OU1	8.41395	-10.8279	-10.122017	3	0.1269317	NA	NA	1.43466416	NA	NA	19.07727	0.03633367
TOL_XMID	OUM	8.845005	-9.69001	-8.477889	4	0.1102553	0.172481	0.1083502	9.94221341	NA	NA	135.18923	0.03290198
TOL_XMID	BM	-19.788275	43.57655	43.919407	2	0.1444837	NA	NA	0.01627966	NA	NA	NA	NA
TOL_XMID	BMM	-18.96063	43.92126	44.627143	3	0.1404507	NA	NA	NA	0.023757	0.01344937	NA	NA

Sowing N. 1 (S1) - Stochastic map : ARD - Treatment : H

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
ASYM	OUM	-169.8616	347.7233	348.9354	4	41.60167	18.51447	75.73046	82.93506	NA	NA	0.06234898	11.70296
ASYM	BM	-173.4666	350.9331	351.276	2	51.40392	NA	NA	53.01059	NA	NA	NA	NA
ASYM	BMM	-172.5955	351.1911	351.8969	3	48.48989	NA	NA	NA	32.24504	64.91073	NA	NA
ASYM	OU1	-172.6938	351.3877	352.0935	3	51.86213	NA	NA	71.83887	NA	NA	0.03141865	22.06165

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
TOL_ASYM	BMM	-57.97728	121.9546	122.6604	3	-0.03509467	NA	NA	NA	0.03383627	0.2220031	NA	NA
TOL_ASYM	OU1	-60.34494	126.6899	127.3958	3	0.21819278	NA	NA	0.3021266	NA	NA	0.07972246	8.694504
TOL_ASYM	OUM	-59.42575	126.8515	128.0636	4	-0.03415176	-0.5279488	0.6812932	0.3184655	NA	NA	0.09272574	7.49322
TOL_ASYM	BM	-63.41573	130.8315	131.1743	2	0.12329547	NA	NA	0.1617576	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
LA	BMM	-269.7498	545.4996	546.2055	3	347.4841	NA	NA	NA	3540.486	13135.62	NA	NA
LA	BM	-272.2662	548.5323	548.8752	2	399.5467	NA	NA	9609.155	NA	NA	NA	NA
LA	OUM	-270.2842	548.5684	549.7805	4	303.3417	21.5502	712.3254	14146.103	NA	NA	0.04623113	15.48158
LA	OU1	-271.8144	549.6288	550.3347	3	406.8153	NA	NA	12986.186	NA	NA	0.02951067	23.48802

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
LDI	OUM	-28.19929	64.39857	65.61069	4	1.890283	1.596673	2.353737	0.0676118	NA	NA	0.10577693	6.672747
LDI	OU1	-30.07237	66.14474	66.85063	3	2.069008	NA	NA	0.05567876	NA	NA	0.06794279	10.201924
LDI	BM	-32.61289	69.22577	69.56863	2	2.054505	NA	NA	0.03197314	NA	NA	NA	NA
LDI	BMM	-31.64279	69.28557	69.99145	3	2.006623	NA	NA	NA	0.01992472	0.03885752	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
LDMC	OU1	-128.7909	263.5818	264.2877	3	18.14981	NA	NA	319.72898	NA	NA	3.107117	0.2230837
LDMC	OUM	-127.876	263.7519	264.964	4	17.08785	15.70595	19.25276	16034.57373	NA	NA	162.486712	0.299976
LDMC	BM	-142.185	288.3701	288.7129	2	18.86255	NA	NA	10.21744	NA	NA	NA	NA
LDMC	BMM	-142.0414	290.0828	290.7887	3	18.78659	NA	NA	NA	10.37267	10.29901	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
MGR	OU1	32.008092	-58.016184	-57.3103	3	0.205853	NA	NA	0.02915668	NA	NA	1.334165	0.5195362
MGR	OUM	32.505	-57.010001	-55.79788	4	0.2178841	0.2339604	0.194085	0.046936942	NA	NA	2.212625	0.4128336
MGR	BMM	16.596444	-27.192888	-26.48701	3	0.2004998	NA	NA	NA	0.008879776	0.00091845	NA	NA
MGR	BM	4.405274	-4.810547	-4.46769	2	0.2050837	NA	NA	0.004556578	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
TOL_MGR	OU1	-23.06859	52.13718	52.84306	3	-0.1199156	NA	NA	1.0884197	NA	NA	2.758722	0.2512566
TOL_MGR	OUM	-22.56556	53.13111	54.34323	4	-0.1676942	-0.2325835	-0.06754869	34.0520642	NA	NA	88.583309	0.1027183
TOL_MGR	BMM	-54.83503	115.67006	116.37595	3	-0.1588164	NA	NA	NA	0.06531771	0.1342844	NA	NA
TOL_MGR	BM	-56.1534	116.3068	116.64966	2	-0.1383423	NA	NA	0.1103736	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
RESpT1	OU1	-147.8904	301.7808	302.4867	3	56.73243	NA	NA	47.42497	NA	NA	0.1457837	4.754628
RESpT1	OUM	-146.8433	301.6866	302.8987	4	54.30724	50.57743	59.95597	51.22363	NA	NA	0.1679297	5.010602
RESpT1	BM	-149.7698	303.5396	303.8825	2	55.61755	NA	NA	15.23042	NA	NA	NA	NA
RESpT1	BMM	-149.6336	305.2672	305.9731	3	55.98309	NA	NA	NA	16.90432	14.39659	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
RESpT2	OUM	-159.9927	327.9855	329.1976	4	23.15233	30.69227	11.42957	13535.52611	NA	NA	25.190226	0.3222923
RESpT2	OU1	-164.5282	335.0563	335.7622	3	17.33239	NA	NA	1059.38613	NA	NA	1.563466	0.44334
RESpT2	BMM	-173.8993	353.7986	354.5045	3	15.5428	NA	NA	NA	143.3324	28.29688	NA	NA
RESpT2	BM	-179.1144	362.2288	362.5716	2	17.77633	NA	NA	71.36064	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
SLA	OU1	-141.0174	288.0348	288.7406	3	27.21867	NA	NA	490.62049	NA	NA	2.503313	0.276892
SLA	OUM	-141.001	290.002	291.2141	4	27.29612	27.47392	27.10167	500.50669	NA	NA	2.556127	0.2725983
SLA	BMM	-162.2472	330.4943	331.2002	3	26.1452	NA	NA	NA	59.32637	18.85496	NA	NA
SLA	BM	-165.8988	335.7977	336.1405	2	26.18633	NA	NA	35.59448	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
XMID	OUM	-117.426	242.8519	244.0641	4	-28.3197	-27.09887	-30.2271	4533.897134	NA	NA	79.979103	0.05287239
XMID	OU1	-118.7241	243.4481	244.154	3	-29.31193	NA	NA	559.94685	NA	NA	9.244741	0.07497746
XMID	BM	-140.5041	285.0082	285.351	2	-29.49912	NA	NA	9.352322	NA	NA	NA	NA
XMID	BMM	-139.9509	285.9019	286.6078	3	-29.63769	NA	NA	NA	11.92614	7.93009	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
TOL_XMID	OU1	8.41395	-10.827899	-10.122017	3	-0.1269317	NA	NA	1.43466416	NA	NA	19.07727	0.03633367
TOL_XMID	OUM	8.861359	-9.722718	-8.510596	4	-0.1474749	-0.1731267	-0.1079174	8.45100708	NA	NA	114.91852	0.03409608
TOL_XMID	BM	-19.788275	43.57655	43.919407	2	-0.1444837	NA	NA	0.01627966	NA	NA	NA	NA
TOL_XMID	BMM	-19.567537	45.135075	45.840957	3	-0.1429506	NA	NA	NA	0.01863179	0.0151585	NA	NA

Sowing N. 2 (S2) - Stochastic map : ER - Treatment : C

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
ASYM	OU1	-336.1386	678.2772	678.6015	3	51.36158	NA	NA	97.90604	NA	NA	0.1000066	6.931013
ASYM	OUM	-335.3151	678.6302	679.1782	4	53.66576	41.29195	54.13782	104.9687	NA	NA	0.1154007	6.052639
ASYM	BMM	-341.9252	689.8505	690.1748	3	50.93661	NA	NA	NA	30.0284	64.31059	NA	NA
ASYM	BM	-343.5847	691.1695	691.3295	2	51.51294	NA	NA	54.23241	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
IGR	OUM	127.92578	-247.8516	-247.3036	4	0.583814	0.5637007	0.5844051	0.911880791	NA	NA	206.907549	0.03139508
IGR	OU1	126.35122	-246.7024	-246.3781	3	0.5772806	NA	NA	0.021976086	NA	NA	4.787381	0.14478628
IGR	BMM	82.19705	-158.3941	-158.0698	3	0.5830657	NA	NA	NA	0.001520243	0.000824506	NA	NA
IGR	BM	80.62184	-157.2437	-157.0837	2	0.581239	NA	NA	0.001024231	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
LA	BMM	-538.2698	1082.54	1082.864	3	441.1659	NA	NA	NA	2135.923	13136.69	NA	NA
LA	OUM	-538.2254	1084.451	1084.999	4	534.6508	71.8691	549.8796	15781.032	NA	NA	0.08395761	8.439826
LA	OU1	-541.1008	1088.202	1088.526	3	465.4522	NA	NA	14243.696	NA	NA	0.05946685	11.656027
LA	BM	-544.0776	1092.155	1092.315	2	468.9691	NA	NA	9266.134	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
LDI	OU1	-42.23871	90.47742	90.80175	3	1.790764	NA	NA	0.04593352	NA	NA	0.08007084	8.656674
LDI	OUM	-41.8646	91.72919	92.27714	4	1.813412	1.702791	1.81612	0.04691769	NA	NA	0.08465921	8.222253
LDI	BM	-49.04017	102.08033	102.24033	2	1.812013	NA	NA	0.02846311	NA	NA	NA	NA
LDI	BMM	-48.82173	103.64345	103.96778	3	1.808961	NA	NA	NA	0.03190534	0.02724368	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
LDMC	OUM	-220.0251	448.0502	448.5982	4	18.52727	15.83719	18.61596	19.283594	NA	NA	0.5445529	1.299371
LDMC	OU1	-222.3998	450.7996	451.1239	3	17.78164	NA	NA	16.173355	NA	NA	0.4191566	1.653671
LDMC	BMM	-242.7719	491.5438	491.8681	3	18.23762	NA	NA	NA	6.560133	3.348455	NA	NA
LDMC	BM	-244.9624	493.9248	494.0848	2	18.08218	NA	NA	4.325382	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
SSIZ	OU1	-80.64527	167.2905	167.6149	3	1.072132	NA	NA	0.15267692	NA	NA	0.1147832	6.038751
SSIZ	OUM	-80.41412	168.8282	169.3762	4	1.043427	1.193242	1.03915	0.15318509	NA	NA	0.116395	5.963152
SSIZ	BMM	-84.04954	174.0991	174.4234	3	1.191555	NA	NA	NA	0.1298416	0.05299829	NA	NA
SSIZ	BM	-87.40701	178.814	178.974	2	1.1998	NA	NA	0.07612481	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
LTH	OUM	114.29807	-220.5961	-220.0482	4	0.264795	0.3055017	0.2635633	0.002086226	NA	NA	0.288757	2.410352
LTH	OU1	112.1851	-218.3702	-218.0459	3	0.2749067	NA	NA	0.002049412	NA	NA	0.2651175	2.61449
LTH	BM	95.23649	-186.473	-186.313	2	0.2846388	NA	NA	0.00070413	NA	NA	NA	NA
LTH	BMM	95.36308	-184.7262	-184.4018	3	0.284579	NA	NA	NA	0.000712375	0.000704304	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
MGR	OUM	137.43204	-266.8641	-266.3161	4	0.2411802	0.2147712	0.2419842	0.212493635	NA	NA	61.47587	0.128956
MGR	OU1	134.15752	-262.315	-261.9907	3	0.2325937	NA	NA	0.012082227	NA	NA	3.21004	0.215931
MGR	BMM	88.7473	-171.4946	-171.1703	3	0.2387172	NA	NA	NA	0.001989597	0.000576035	NA	NA
MGR	BM	83.43357	-162.8671	-162.7071	2	0.2348588	NA	NA	0.000952988	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
NLEA	OU1	-293.6943	593.3886	593.713	3	15.90802	NA	NA	32.43885	NA	NA	0.09737636	7.118229
NLEA	OUM	-293.3066	594.6133	595.1612	4	16.7026	11.50117	16.91658	32.00877	NA	NA	0.0968177	7.161253
NLEA	BM	-298.693	601.386	601.546	2	14.52655	NA	NA	17.15361	NA	NA	NA	NA
NLEA	BMM	-298.1975	602.395	602.7194	3	14.3423	NA	NA	NA	14.08411	18.49112	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
RESmT1	OU1	-262.3717	530.7433	531.0677	3	74.84054	NA	NA	47.62795	NA	NA	0.4459235	1.554408
RESmT1	OUM	-261.7334	531.4668	532.0148	4	74.23755	76.54441	74.1552	44.09362	NA	NA	0.4162927	1.669823
RESmT1	BMM	-282.0043	570.0087	570.333	3	75.73249	NA	NA	NA	4.555813	15.62564	NA	NA
RESmT1	BM	-286.7656	577.5311	577.6911	2	75.16827	NA	NA	12.63381	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
RESmT2	OU1	-312.8318	631.6636	631.9879	3	60.55544	NA	NA	578.69874	NA	NA	1.603508	0.4322692
RESmT2	OUM	-312.3641	632.7283	633.2762	4	61.55509	58.24371	61.66064	782.67723	NA	NA	2.195596	0.5254307
RESmT2	BMM	-341.6995	689.399	689.7233	3	57.14854	NA	NA	NA	87.57303	41.15525	NA	NA
RESmT2	BM	-344.5781	693.1562	693.3162	2	56.6092	NA	NA	55.63152	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
RESpT1	OU1	-288.6444	583.2888	583.6131	3	67.97212	NA	NA	625.35712	NA	NA	3.253294	0.2130601
RESpT1	OUM	-288.5794	585.1588	585.7067	4	67.73646	68.49336	67.70767	626.42478	NA	NA	3.26429	0.2124503
RESpT1	BMM	-343.6128	693.2257	693.55	3	67.91793	NA	NA	NA	33.87216	65.80039	NA	NA
RESpT1	BM	-345.4317	694.8634	695.0234	2	67.92187	NA	NA	56.86252	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
RESpT2	OUM	-258.7985	525.5971	526.145	4	11.062821	6.694193	11.19235	2130.09767	NA	NA	23.78875	0.36675155
RESpT2	OU1	-262.0758	530.1516	530.476	3	9.629785	NA	NA	3186.81973	NA	NA	32.8399	0.02110686
RESpT2	BM	-293.7903	591.5806	591.7406	2	9.934364	NA	NA	15.12726	NA	NA	NA	NA
RESpT2	BMM	-293.6781	593.3561	593.6805	3	9.955711	NA	NA	NA	16.08205	14.83614	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
SLA	OU1	-267.9482	541.8963	542.2207	3	25.78422	NA	NA	56.18084	NA	NA	0.4571121	1.516361
SLA	OUM	-267.8643	543.7285	544.2765	4	25.87969	25.50616	25.89742	55.30798	NA	NA	0.4502256	1.540976
SLA	BMM	-289.753	585.506	585.8304	3	25.17086	NA	NA	NA	25.98065	10.27219	NA	NA
SLA	BM	-293.9576	591.9151	592.0751	2	25.07603	NA	NA	15.19228	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
TGER	OUM	-148.3423	304.6846	305.2325	4	16.00232	17.47129	15.95709	2.3295599	NA	NA	0.4011743	1.743977
TGER	OU1	-151.7915	309.5829	309.9073	3	16.39118	NA	NA	1.8068428	NA	NA	0.2694883	2.572086
TGER	BM	-168.9003	341.8006	341.9606	2	17.11002	NA	NA	0.6151993	NA	NA	NA	NA
TGER	BMM	-168.4759	342.9519	343.2762	3	17.07599	NA	NA	NA	0.7286051	0.5753365	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
XMID	OU1	-205.3023	416.6045	416.9288	3	-22.72697	NA	NA	22.897039	NA	NA	0.9825977	0.7054231

XMID	OUM	-205.0213	418.0427	418.5906	4	-22.53668	-23.17446	-22.52046	23.912183	NA	NA	1.0359507	0.6713404
XMID	BMM	-224.9741	455.9483	456.2726	3	-21.93489	NA	NA	NA	8.157274	1.493471	NA	NA
XMID	BM	-237.9428	479.8857	480.0457	2	-21.86073	NA	NA	3.612904	NA	NA	NA	NA

Sowing N. 2 (S2) - Stochastic map : ARD - Treatment : C

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
ASYM	OU1	-336.1386	678.2772	678.6015	3	51.36158	NA	NA	97.90604	NA	NA	0.1000066	6.931013
ASYM	OUM	-335.0847	678.1695	678.7174	4	47.44678	42.21928	56.34195	106.36699	NA	NA	0.1187837	5.874576
ASYM	BMM	-341.0631	688.1262	688.4506	3	50.43979	NA	NA	NA	29.25085	69.12304	NA	NA
ASYM	BM	-343.5847	691.1695	691.3295	2	51.51294	NA	NA	54.23241	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
IGR	OUM	127.94798	-247.896	-247.348	4	0.5717736	0.5636174	0.5844456	0.656333528	NA	NA	148.933533	0.03715481
IGR	OU1	126.35122	-246.7024	-246.3781	3	0.5772806	NA	NA	0.021976086	NA	NA	4.787381	0.14478628
IGR	BM	80.62184	-157.2437	-157.0837	2	0.581239	NA	NA	0.001024231	NA	NA	NA	NA
IGR	BMM	81.18108	-156.3622	-156.0378	3	0.582029	NA	NA	NA	0.001222968	0.000921224	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
LA	BMM	-538.0349	1082.07	1082.394	3	419.1391	NA	NA	NA	2826.599	14261.5	NA	NA
LA	OUM	-538.2989	1084.598	1085.146	4	370.068	198.506	622.0313	16254.062	NA	NA	0.0880237	8.047461
LA	OU1	-541.1008	1088.202	1088.526	3	465.4522	NA	NA	14243.696	NA	NA	0.05946685	11.656027
LA	BM	-544.0776	1092.155	1092.315	2	468.9691	NA	NA	9266.134	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
LDI	OU1	-42.23871	90.47742	90.80175	3	1.790764	NA	NA	0.04593352	NA	NA	0.08007084	8.656674
LDI	OUM	-41.8826	91.76519	92.31314	4	1.763961	1.723147	1.830327	0.04669025	NA	NA	0.08387248	8.303518
LDI	BM	-49.04017	102.08033	102.24033	2	1.812013	NA	NA	0.02846311	NA	NA	NA	NA
LDI	BMM	-48.9199	103.8398	104.16412	3	1.807546	NA	NA	NA	0.0275743	0.0292522	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
LDMC	OUM	-220.0748	448.1495	448.6974	4	17.01823	15.95336	18.65856	19.282868	NA	NA	0.5440845	1.293814
LDMC	OU1	-222.3998	450.7996	451.1239	3	17.78164	NA	NA	16.173355	NA	NA	0.4191566	1.653671
LDMC	BM	-244.9624	493.9248	494.0848	2	18.08218	NA	NA	4.325382	NA	NA	NA	NA
LDMC	BMM	-244.0762	494.1524	494.4767	3	18.21029	NA	NA	NA	5.434056	3.678519	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
SSIZ	OU1	-80.64527	167.2905	167.6149	3	1.072132	NA	NA	0.15267692	NA	NA	0.1147832	6.038751
SSIZ	OUM	-80.39359	168.7872	169.3351	4	1.104679	1.15409	1.025825	0.15267524	NA	NA	0.115911	5.986518
SSIZ	BMM	-84.72609	175.4522	175.7765	3	1.190253	NA	NA	NA	0.1145747	0.05275766	NA	NA
SSIZ	BM	-87.40701	178.814	178.974	2	1.1998	NA	NA	0.07612481	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
LTH	OUM	113.9733	-219.9466	-219.3987	4	0.285631	0.300042	0.262986	0.002137658	NA	NA	0.294243	2.367737
LTH	OU1	112.1851	-218.3702	-218.0459	3	0.2749067	NA	NA	0.002049412	NA	NA	0.2651175	2.61449
LTH	BM	95.23649	-186.473	-186.313	2	0.2846388	NA	NA	0.00070413	NA	NA	NA	NA
LTH	BMM	95.65374	-185.3075	-184.9831	3	0.2854157	NA	NA	NA	0.000613119	0.000769149	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
MGR	OUM	137.41745	-266.8349	-266.2869	4	0.2255268	0.2149109	0.24199	0.07606566	NA	NA	22.00588	0.1327053
MGR	OU1	134.15752	-262.315	-261.9907	3	0.2325937	NA	NA	0.012082227	NA	NA	3.21004	0.215931
MGR	BMM	86.45816	-166.9163	-166.592	3	0.237423	NA	NA	NA	0.001494153	0.000658691	NA	NA
MGR	BM	83.43357	-162.8671	-162.7071	2	0.2348588	NA	NA	0.000952988	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
NLEA	OU1	-293.6943	593.3886	593.713	3	15.90802	NA	NA	32.43885	NA	NA	0.09737636	7.118229
NLEA	OUM	-293.3247	594.6495	595.1974	4	14.75969	13.00227	17.63582	31.94132	NA	NA	0.09640324	7.193939
NLEA	BMM	-297.3506	600.7011	601.0254	3	14.30503	NA	NA	NA	12.23672	20.0871	NA	NA
NLEA	BM	-298.693	601.386	601.546	2	14.52655	NA	NA	17.15361	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
RESmT1	OU1	-262.3717	530.7433	531.0677	3	74.84054	NA	NA	47.62795	NA	NA	0.4459235	1.554408
RESmT1	OUM	-261.8827	531.7655	532.3134	4	75.43739	76.23495	74.19138	45.44549	NA	NA	0.428929	1.62036
RESmT1	BMM	-279.2713	564.5426	564.8669	3	75.96021	NA	NA	NA	4.084518	16.99506	NA	NA
RESmT1	BM	-286.7656	577.5311	577.6911	2	75.16827	NA	NA	12.63381	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
RESmT2	OU1	-312.8318	631.6636	631.9879	3	60.55544	NA	NA	578.69874	NA	NA	1.603508	0.4322692
RESmT2	OUM	-312.3336	632.6672	633.2151	4	59.53438	58.22244	61.71725	508.14917	NA	NA	1.417755	0.5565517
RESmT2	BMM	-343.2763	692.5526	692.8769	3	56.63603	NA	NA	NA	72.62615	45.29401	NA	NA
RESmT2	BM	-344.5781	693.1562	693.3162	2	56.6092	NA	NA	55.63152	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
RESpT1	OU1	-288.6444	583.2888	583.6131	3	67.97212	NA	NA	625.35712	NA	NA	3.253294	0.2130601
RESpT1	OUM	-288.5718	585.1436	585.6916	4	68.21495	68.53736	67.68213	626.00397	NA	NA	3.262749	0.2125444
RESpT1	BMM	-341.4508	688.9016	689.226	3	67.97453	NA	NA	NA	28.45772	71.69245	NA	NA
RESpT1	BM	-345.4317	694.8634	695.0234	2	67.92187	NA	NA	56.86252	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
RESpT2	OUM	-258.7227	525.4455	525.9934	4	8.484883	6.688183	11.24342	886.57801	NA	NA	9.896448	0.39744823
RESpT2	OU1	-262.0758	530.1516	530.476	3	9.629785	NA	NA	3186.81973	NA	NA	32.839903	0.02110686
RESpT2	BM	-293.7903	591.5806	591.7406	2	9.934364	NA	NA	15.12726	NA	NA	NA	NA
RESpT2	BMM	-293.4855	592.9709	593.2952	3	9.842621	NA	NA	NA	13.57149	16.20113	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
SLA	OU1	-267.9482	541.8963	542.2207	3	25.78422	NA	NA	56.18084	NA	NA	0.4571121	1.516361
SLA	OUM	-267.8805	543.761	544.3089	4	25.7301	25.59425	25.868	55.49133	NA	NA	0.4517017	1.535215
SLA	BMM	-291.7705	589.541	589.8653	3	25.0341	NA	NA	NA	21.34659	11.33379	NA	NA
SLA	BM	-293.9576	591.9151	592.0751	2	25.07603	NA	NA	15.19228	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
TGER	OUM	-148.1832	304.3664	304.9143	4	16.83582	17.40134	15.90733	2.3359083	NA	NA	0.4039482	1.738421
TGER	OU1	-151.7915	309.5829	309.9073	3	16.39118	NA	NA	1.8068428	NA	NA	0.2694883	2.572086
TGER	BM	-168.9003	341.8006	341.9606	2	17.11002	NA	NA	0.6151993	NA	NA	NA	NA
TGER	BMM	-168.5413	343.0827	343.407	3	17.10419	NA	NA	NA	0.600479	0.6323354	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
XMID	OU1	-205.3023	416.6045	416.9288	3	-22.72697	NA	NA	22.897039	NA	NA	0.9825977	0.7054231
XMID	OUM	-204.9934	417.9869	418.5348	4	-22.91215	-23.17845	-22.50384	23.720669	NA	NA	1.0280262	0.6761382
XMID	BMM	-229.0437	464.0874	464.4117	3	-21.7308	NA	NA	NA	6.493019	1.663139	NA	NA
XMID	BM	-237.9428	479.8857	480.0457	2	-21.86073	NA	NA	3.612904	NA	NA	NA	NA

Sowing N. 2 (S2) - Stochastic map : ER - Treatment : F

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
ASYM	OUM	-313.7786	635.5572	636.1369	4	50.24888	31.17775	50.86477	119.39866	NA	NA	0.1580226	4.468101
ASYM	OU1	-316.1855	638.3709	638.7138	3	46.18057	NA	NA	103.22145	NA	NA	0.1157948	5.985994
ASYM	BMM	-322.6545	651.309	651.6519	3	46.99779	NA	NA	NA	25.77894	69.44791	NA	NA
ASYM	BM	-325.6497	655.2993	655.4684	2	47.65528	NA	NA	57.09698	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
TOL_ASYM	OUM	11.87152	-15.74303	-15.16332	4	-0.05676805	-0.1362899	-0.05431364	10.62703167	NA	NA	125.05032	0.02296719
TOL_ASYM	OU1	10.59275	-15.1855	-14.84264	3	-0.08199826	NA	NA	3.76625745	NA	NA	42.82413	0.0161859
TOL_ASYM	BM	-53.35442	110.70884	110.87786	2	-0.06395703	NA	NA	0.03634932	NA	NA	NA	NA
TOL_ASYM	BMM	-53.15939	112.31878	112.66163	3	-0.06474035	NA	NA	NA	0.04041688	0.03491872	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
IGR	OU1	130.07538	-254.1508	-253.8079	3	0.5734273	NA	NA	0.098300929	NA	NA	28.22819	0.02455514
IGR	OUM	130.11725	-252.2345	-251.6548	4	0.5743414	0.5714576	0.5744289	0.575254939	NA	NA	165.40628	0.02433733
IGR	BMM	74.0891	-142.1782	-141.8353	3	0.5683949	NA	NA	NA	0.000644965	0.001471316	NA	NA
IGR	BM	71.74141	-139.4828	-139.3138	2	0.5677718	NA	NA	0.001236404	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
TOL_IGR	OU1	50.848543	-95.69709	-95.35423	3	0.021744508	NA	NA	0.078580274	NA	NA	2.64089	0.2624673
TOL_IGR	OUM	51.605228	-95.21046	-94.63075	4	0.009772912	0.04715098	0.008682465	0.223538851	NA	NA	7.671596	0.2489971
TOL_IGR	BM	9.770053	-15.54011	-15.37109	2	0.0109526	NA	NA	0.006600257	NA	NA	NA	NA

TOL_IGR	BMM	10.094287	-14.18857	-13.84572	3	0.01132402	NA	NA	NA	0.006587689	0.006666774	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
LA	OUM	-521.857	1051.714	1052.294	4	460.9366	206.3882	469.3855	46972.45	NA	NA	0.2492825	2.818542
LA	OU1	-524.469	1054.938	1055.281	3	402.404	NA	NA	39419.36	NA	NA	0.1816624	3.815579
LA	BMM	-536.273	1078.546	1078.889	3	451.427	NA	NA	NA	11410.82	20256.84	NA	NA
LA	BM	-537.6466	1079.293	1079.462	2	455.1425	NA	NA	17577.91	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
LDI	OU1	-57.54345	121.0869	121.4298	3	1.82502	NA	NA	0.07898844	NA	NA	0.08485772	8.168346
LDI	OUM	-57.1057	122.2114	122.7911	4	1.84832	1.748678	1.848887	0.0802471	NA	NA	0.08917343	7.795731
LDI	BM	-63.87428	131.7486	131.9176	2	1.894041	NA	NA	0.0483031	NA	NA	NA	NA
LDI	BMM	-63.18963	132.3793	132.7221	3	1.887676	NA	NA	NA	0.03820542	0.05264748	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
LDMC	OUM	-204.0002	416.0004	416.5801	4	19.7475	16.55461	19.8488	52.058231	NA	NA	1.7342978	0.6245982
LDMC	OU1	-208.4872	422.9745	423.3173	3	18.83153	NA	NA	26.736077	NA	NA	0.7779838	0.8909532
LDMC	BMM	-231.2937	468.5874	468.9303	3	19.23897	NA	NA	NA	2.582927	5.543652	NA	NA
LDMC	BM	-233.2669	470.5338	470.7028	2	19.52739	NA	NA	4.701678	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
LTH	OU1	106.90522	-207.8104	-207.4676	3	0.2950067	NA	NA	0.055579496	NA	NA	8.533956	0.08122226
LTH	OUM	107.10346	-206.2069	-205.6272	4	0.2920208	0.3009856	0.2917394	0.039748882	NA	NA	6.132989	0.11774006
LTH	BMM	65.239	-124.478	-124.1351	3	0.2936417	NA	NA	NA	0.000632369	0.002061064	NA	NA
LTH	BM	61.16623	-118.3325	-118.1634	2	0.2914398	NA	NA	0.001645465	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
MGR	OU1	78.94484	-151.88969	-151.54683	3	0.2404544	NA	NA	0.328082968	NA	NA	23.66251	0.02929306
MGR	OUM	79.25402	-150.50803	-149.92832	4	0.2455951	0.2295317	0.2460843	0.90508393	NA	NA	65.61181	0.1049523
MGR	BM	29.14794	-54.29589	-54.12687	2	0.2288246	NA	NA	0.003909392	NA	NA	NA	NA
MGR	BMM	29.97494	-53.94988	-53.60702	3	0.2298659	NA	NA	NA	0.005013598	0.003523478	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
TOL_MGR	OU1	-39.8947	85.78939	86.13225	3	0.1030916	NA	NA	2.1477465	NA	NA	6.238122	0.11111472
TOL_MGR	OUM	-39.79089	87.58178	88.16149	4	0.09180048	0.1250408	0.09083854	9.8743107	NA	NA	28.762713	0.06641847
TOL_MGR	BMM	-94.19074	194.38147	194.72433	3	0.045369	NA	NA	NA	0.2005295	0.1083067	NA	NA
TOL_MGR	BM	-98.33562	200.67123	200.84025	2	0.04598305	NA	NA	0.1225947	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
NLEA	OU1	-271.8088	549.6177	549.9605	3	14.7388	NA	NA	43.76748	NA	NA	0.1878978	3.688958
NLEA	OUM	-271.4064	550.8127	551.3924	4	15.47673	12.079	15.5946	42.90652	NA	NA	0.1856613	3.734772
NLEA	BMM	-281.9821	569.9643	570.3071	3	13.56005	NA	NA	NA	11.67129	20.84168	NA	NA
NLEA	BM	-283.353	570.7061	570.8751	2	13.94006	NA	NA	18.20323	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
RESmT2	OU1	-297.8565	601.7131	602.0559	3	58.24823	NA	NA	283.91007	NA	NA	0.7349479	0.9431242
RESmT2	OUM	-297.5376	603.0753	603.655	4	57.37547	60.33055	57.29227	279.54938	NA	NA	0.72952	0.9561371
RESmT2	BM	-319.1008	642.2017	642.3707	2	56.78906	NA	NA	47.83491	NA	NA	NA	NA
RESmT2	BMM	-318.9421	643.8843	644.2271	3	56.73458	NA	NA	NA	52.63478	46.21971	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
SLA	OU1	-236.0316	478.0631	478.406	3	22.32439	NA	NA	70.90824	NA	NA	0.9951474	0.6965272
SLA	OUM	-235.9637	479.9274	480.5071	4	22.19961	22.61329	22.1893	71.51543	NA	NA	1.0061004	0.6893184
SLA	BMM	-269.2117	544.4234	544.7663	3	21.15445	NA	NA	NA	6.338833	16.16172	NA	NA
SLA	BM	-272.2658	548.5315	548.7005	2	21.18719	NA	NA	13.48992	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
XMID	OU1	-192.2286	390.4571	390.8	3	-21.99063	NA	NA	318.569336	NA	NA	15.0775	0.04597228
XMID	OUM	-192.0889	392.1778	392.7575	4	-21.85294	-22.27653	-21.8404	461.361862	NA	NA	21.90982	0.07641286
XMID	BM	-232.0834	468.1667	468.3357	2	-21.30592	NA	NA	4.553664	NA	NA	NA	NA
XMID	BMM	-231.9822	469.9644	470.3073	3	-21.31171	NA	NA	NA	4.656256	4.547246	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
TOL_XMID	OU1	33.35674	-60.71347	-60.37061	3	0.02615623	NA	NA	1.22173564	NA	NA	25.70136	0.02696928
TOL_XMID	OUM	33.5086	-59.01721	-58.4375	4	0.01971229	0.04000216	0.01909321	11.21452955	NA	NA	236.86541	0.01861498
TOL_XMID	BMM	-15.68623	37.37247	37.71532	3	0.02764158	NA	NA	NA	0.01835049	0.01148608	NA	NA
TOL_XMID	BM	-16.81056	37.62112	37.79014	2	0.02733342	NA	NA	0.01353804	NA	NA	NA	NA

Sowing N. 2 (S2) - Stochastic map : ARD - Treatment : F

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
ASYM	OUM	-313.4675	634.9351	635.5148	4	40.67946	32.65587	52.94225	121.50524	NA	NA	0.1635024	4.288118
ASYM	OU1	-316.1855	638.3709	638.7138	3	46.18057	NA	NA	103.22145	NA	NA	0.1157948	5.985994
ASYM	BMM	-321.1238	648.2477	648.5905	3	45.84075	NA	NA	NA	24.0211	75.16301	NA	NA
ASYM	BM	-325.6497	655.2993	655.4684	2	47.65528	NA	NA	57.09698	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
TOL_ASYM	OUM	11.87964	-15.75928	-15.17957	4	-0.1043412	-0.1364349	-0.05421031	6.55380417	NA	NA	77.1231	0.02546579
TOL_ASYM	OU1	10.59275	-15.1855	-14.84264	3	-0.08199826	NA	NA	3.76625745	NA	NA	42.82413	0.0161859
TOL_ASYM	BM	-53.35442	110.70884	110.87786	2	-0.06395703	NA	NA	0.03634932	NA	NA	NA	NA
TOL_ASYM	BMM	-53.08728	112.17456	112.51741	3	-0.06455991	NA	NA	NA	0.03332268	0.03851989	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
IGR	OU1	130.07538	-254.1508	-253.8079	3	0.5734273	NA	NA	0.098300929	NA	NA	28.22819	0.02455514
IGR	OUM	130.11745	-252.2349	-251.6552	4	0.5726011	0.5714453	0.5744375	0.31192719	NA	NA	89.69282	0.02216273
IGR	BMM	76.40391	-146.8078	-146.465	3	0.5688332	NA	NA	NA	0.000534876	0.001616204	NA	NA
IGR	BM	71.74141	-139.4828	-139.3138	2	0.5677718	NA	NA	0.001236404	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
TOL_IGR	OU1	50.848543	-95.69709	-95.35423	3	0.02174451	NA	NA	0.078580274	NA	NA	2.64089	0.2624673
TOL_IGR	OUM	51.600453	-95.20091	-94.6212	4	0.03142536	0.04675879	0.008426648	0.302970422	NA	NA	10.40174	0.2323126
TOL_IGR	BM	9.770053	-15.54011	-15.37109	2	0.0109526	NA	NA	0.006600257	NA	NA	NA	NA
TOL_IGR	BMM	10.571922	-15.14384	-14.80099	3	0.01395248	NA	NA	NA	0.005340916	0.007405009	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
LA	OUM	-521.7692	1051.538	1052.118	4	328.9695	219.6103	484.1614	47677.63	NA	NA	0.2544665	2.760469
LA	OU1	-524.469	1054.938	1055.281	3	402.404	NA	NA	39419.36	NA	NA	0.1816624	3.815579
LA	BMM	-535.3742	1076.748	1077.091	3	443.6264	NA	NA	NA	10141.82	21882.98	NA	NA
LA	BM	-537.6466	1079.293	1079.462	2	455.1425	NA	NA	17577.91	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
LDI	OU1	-57.54345	121.0869	121.4298	3	1.82502	NA	NA	0.07898844	NA	NA	0.08485772	8.168346
LDI	OUM	-57.19868	122.3974	122.9771	4	1.819467	1.783101	1.839323	0.07940192	NA	NA	0.08712015	7.982862
LDI	BMM	-62.63935	131.2787	131.6216	3	1.877637	NA	NA	NA	0.0340835	0.05647413	NA	NA
LDI	BM	-63.87428	131.7486	131.9176	2	1.894041	NA	NA	0.0483031	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
LDMC	OUM	-203.9525	415.9049	416.4846	4	17.88054	16.59336	19.87534	35.803424	NA	NA	1.2018846	0.6193792
LDMC	OU1	-208.4872	422.9745	423.3173	3	18.83153	NA	NA	26.736077	NA	NA	0.7779838	0.8909532
LDMC	BMM	-229.4355	464.871	465.2139	3	18.99988	NA	NA	NA	2.230668	6.058893	NA	NA
LDMC	BM	-233.2669	470.5338	470.7028	2	19.52739	NA	NA	4.701678	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
LTH	OU1	106.90522	-207.8104	-207.4676	3	0.2950067	NA	NA	0.055579496	NA	NA	8.533956	0.08122226
LTH	OUM	107.1063	-206.2126	-205.6329	4	0.2974038	0.3011108	0.291607	0.05567937	NA	NA	8.58461	0.12519836
LTH	BMM	67.87552	-129.751	-129.4082	3	0.2970866	NA	NA	NA	0.000534604	0.002287081	NA	NA
LTH	BM	61.16623	-118.3325	-118.1634	2	0.2914398	NA	NA	0.001645465	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
MGR	OU1	78.94484	-151.88969	-151.54683	3	0.2404544	NA	NA	0.328082968	NA	NA	23.66251	0.02929306
MGR	OUM	79.22508	-150.45015	-149.87044	4	0.2361177	0.2300905	0.2458524	0.535980652	NA	NA	38.85825	0.09859888
MGR	BM	29.14794	-54.29589	-54.12687	2	0.2288246	NA	NA	0.003909392	NA	NA	NA	NA
MGR	BMM	29.78406	-53.56812	-53.22526	3	0.2288197	NA	NA	NA	0.00388029	0.003995691	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life

TOL_MGR	OU1	-39.8947	85.78939	86.13225	3	0.1030916	NA	NA	2.1477465	NA	NA	6.238122	0.11111472
TOL_MGR	OUM	-39.79672	87.59344	88.17315	4	0.11195789	0.1267817	0.08997476	7.7211846	NA	NA	22.489867	0.07047582
TOL_MGR	BMM	-94.34925	194.69849	195.04135	3	0.04613365	NA	NA	NA	0.1292814	0.1308827	NA	NA
TOL_MGR	BM	-98.33562	200.67123	200.84025	2	0.04598305	NA	NA	0.1225947	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
NLEA	OU1	-271.8088	549.6177	549.9605	3	14.7388	NA	NA	43.76748	NA	NA	0.1878978	3.688958
NLEA	OUM	-271.5033	551.0066	551.5863	4	13.8896	12.80325	15.74005	43.11719	NA	NA	0.1862254	3.723385
NLEA	BMM	-280.257	566.5139	566.8568	3	13.39135	NA	NA	NA	9.742023	22.84782	NA	NA
NLEA	BM	-283.353	570.7061	570.8751	2	13.94006	NA	NA	18.20323	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
RESmT2	OU1	-297.8565	601.7131	602.0559	3	58.24823	NA	NA	283.91007	NA	NA	0.7349479	0.9431242
RESmT2	OUM	-297.5399	603.0797	603.6594	4	59.12992	60.2015	57.27538	277.66442	NA	NA	0.7241024	0.9641071
RESmT2	BM	-319.1008	642.2017	642.3707	2	56.78906	NA	NA	47.83491	NA	NA	NA	NA
RESmT2	BMM	-318.8743	643.7487	644.0916	3	56.88063	NA	NA	NA	44.06876	50.56427	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
SLA	OU1	-236.0316	478.0631	478.406	3	22.32439	NA	NA	70.90824	NA	NA	0.9951474	0.6965272
SLA	OUM	-235.9491	479.8983	480.478	4	22.45792	22.64536	22.16269	71.48622	NA	NA	1.0060734	0.689199
SLA	BMM	-266.8794	539.7588	540.1016	3	21.27368	NA	NA	NA	5.459877	17.57149	NA	NA
SLA	BM	-272.2658	548.5315	548.7005	2	21.18719	NA	NA	13.48992	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
XMID	OU1	-192.2286	390.4571	390.8	3	-21.99063	NA	NA	318.569336	NA	NA	15.0775	0.04597228
XMID	OUM	-192.0863	392.1725	392.7522	4	-22.10682	-22.27694	-21.83815	502.873495	NA	NA	23.88009	0.07989342
XMID	BM	-232.0834	468.1667	468.3357	2	-21.30592	NA	NA	4.553664	NA	NA	NA	NA
XMID	BMM	-231.6381	469.2762	469.6191	3	-21.32271	NA	NA	NA	3.8825	4.986174	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
TOL_XMID	OU1	33.35674	-60.71347	-60.37061	3	0.02615623	NA	NA	1.22173564	NA	NA	25.70136	0.02696928
TOL_XMID	OUM	33.50985	-59.01971	-58.44	4	0.0319277	0.04004752	0.01905857	4.22996789	NA	NA	89.34311	0.02029651
TOL_XMID	BM	-16.81056	37.62112	37.79014	2	0.02733342	NA	NA	0.01353804	NA	NA	NA	NA
TOL_XMID	BMM	-16.513	39.02599	39.36885	3	0.02709103	NA	NA	NA	0.01516065	0.01271139	NA	NA

Sowing N. 2 (S2) - Stochastic map : ER - Treatment : H

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
ASYM	OUM	-341.7568	691.5135	692.0769	4	63.12328	28.21969	64.19455	298.9294	NA	NA	0.2714201	2.730292
ASYM	OU1	-347.6925	701.3851	701.7184	3	54.56125	NA	NA	190.852	NA	NA	0.1239679	5.591343
ASYM	BMM	-357.9459	721.8917	722.225	3	52.61022	NA	NA	NA	49.5952	127.0273	NA	NA
ASYM	BM	-360.5413	725.0826	725.247	2	54.35073	NA	NA	106.3548	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
TOL_ASYM	OUM	-111.8134	231.6268	232.1902	4	0.7392657	-0.3242282	0.7710102	1.9936753	NA	NA	0.8644794	0.8076869
TOL_ASYM	OU1	-117.825	241.65	241.9833	3	0.4335541	NA	NA	1.7958177	NA	NA	0.6534058	1.0608219
TOL_ASYM	BMM	-149.4025	304.805	305.1384	3	0.2977523	NA	NA	NA	0.21758	0.5195974	NA	NA
TOL_ASYM	BM	-152.2036	308.4072	308.5716	2	0.3895452	NA	NA	0.4422895	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
IGR	OU1	99.52526	-193.0505	-192.7172	3	0.5766931	NA	NA	0.216769455	NA	NA	25.4035	0.0272855
IGR	OUM	99.52695	-191.0539	-190.4905	4	0.5769159	0.5761882	0.5769243	0.195153573	NA	NA	22.87116	0.03251935
IGR	BM	54.72913	-105.4583	-105.2939	2	0.5738896	NA	NA	0.001908592	NA	NA	NA	NA
IGR	BMM	55.15285	-104.3057	-103.9724	3	0.5743207	NA	NA	NA	0.002321831	0.001762396	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
TOL_IGR	OU1	27.753	-49.50599	-49.17266	3	0.02170286	NA	NA	1.25163397	NA	NA	22.18821	0.03123944
TOL_IGR	OUM	27.78115	-47.56231	-46.99893	4	0.01889235	0.02847072	0.01860148	9.34653861	NA	NA	165.79853	0.0240555
TOL_IGR	BMM	-35.5076	77.0152	77.34854	3	0.03241158	NA	NA	NA	0.01126102	0.0255431	NA	NA
TOL_IGR	BM	-38.04107	80.08214	80.24653	2	0.03537018	NA	NA	0.02192631	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
LA	OUM	-553.7904	1115.581	1116.144	4	597.9034	171.2101	611.1042	269011.64	NA	NA	1.013159	1.521086
LA	OU1	-558.8595	1123.719	1124.052	3	498.3898	NA	NA	61703.51	NA	NA	0.168527	4.112973
LA	BMM	-559.0295	1124.059	1124.392	3	500.1552	NA	NA	NA	1839.923	39493.03	NA	NA
LA	BM	-573.506	1151.012	1151.176	2	538.2755	NA	NA	28886.09	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
LDI	OUM	-57.72044	123.4409	124.0043	4	2.011146	1.545021	2.025411	0.09958779	NA	NA	0.1377805	5.08369
LDI	OU1	-59.22021	124.4404	124.7738	3	1.912012	NA	NA	0.08980137	NA	NA	0.1115596	6.213245
LDI	BM	-69.28806	142.5761	142.7405	2	1.947489	NA	NA	0.04989777	NA	NA	NA	NA
LDI	BMM	-68.32748	142.655	142.9883	3	1.930736	NA	NA	NA	0.03531767	0.05548823	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
LDMC	OUM	-204.6792	417.3584	417.9217	4	16.05586	12.53217	16.16831	19.417568	NA	NA	0.6935702	1.648684
LDMC	OU1	-208.9601	423.9201	424.2534	3	15.14738	NA	NA	8.796182	NA	NA	0.261853	2.647085
LDMC	BMM	-221.2286	448.4572	448.7905	3	15.24468	NA	NA	NA	1.208959	3.618512	NA	NA
LDMC	BM	-224.4446	452.8892	453.0536	2	15.45651	NA	NA	2.960294	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
LTH	OU1	112.18552	-218.371	-218.0377	3	0.2675458	NA	NA	0.130723191	NA	NA	21.37728	0.03242448
LTH	OUM	112.21746	-216.4349	-215.8715	4	0.2660504	0.2708622	0.2658974	0.130432629	NA	NA	21.32583	0.16942859
LTH	BM	68.25048	-132.501	-132.3366	2	0.2626811	NA	NA	0.001337151	NA	NA	NA	NA
LTH	BMM	68.6438	-131.2876	-130.9543	3	0.2630827	NA	NA	NA	0.001087672	0.001436155	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
MGR	OU1	-45.67195	97.34389	97.67723	3	0.6541839	NA	NA	0.28128003	NA	NA	0.6858438	1.0106488
MGR	OUM	-44.93232	97.86465	98.42803	4	0.6126281	0.7613834	0.6079015	0.28434776	NA	NA	0.7085073	0.9807778
MGR	BMM	-60.4603	126.9206	127.25393	3	0.6140271	NA	NA	NA	0.1337903	0.02297671	NA	NA
MGR	BM	-73.12527	150.25054	150.41493	2	0.6575898	NA	NA	0.05519959	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
TOL_MGR	OUM	-155.2938	318.5877	319.151	4	1.555521	2.457134	1.528305	6.134728	NA	NA	0.8466476	0.8253831
TOL_MGR	OU1	-156.8123	319.6247	319.958	3	1.811094	NA	NA	5.910326	NA	NA	0.7802977	0.8883112
TOL_MGR	BMM	-172.7578	351.5156	351.8489	3	1.585078	NA	NA	NA	2.529112	0.4426797	NA	NA
TOL_MGR	BM	-186.2489	376.4978	376.6622	2	1.82147	NA	NA	1.083437	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
NLEA	OU1	-282.5824	571.1648	571.4981	3	14.45613	NA	NA	32.85245	NA	NA	0.1157572	5.987942
NLEA	OUM	-282.2783	572.5566	573.12	4	15.06332	11.61048	15.19256	32.60897	NA	NA	0.1158511	5.984083
NLEA	BM	-289.0769	582.1538	582.3182	2	13.22124	NA	NA	16.21827	NA	NA	NA	NA
NLEA	BMM	-288.5609	583.1218	583.4551	3	13.09202	NA	NA	NA	13.69703	17.25225	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
RESpT2	OU1	-306.708	619.4161	619.7494	3	19.94326	NA	NA	3428.6116	NA	NA	9.146282	0.07578458
RESpT2	OUM	-305.709	619.418	619.9814	4	18.56285	23.22799	18.4225	31762.1941	NA	NA	86.895045	0.0553435
RESpT2	BMM	-366.1842	738.3684	738.7017	3	19.07065	NA	NA	NA	60.62727	158.7167	NA	NA
RESpT2	BM	-369.4099	742.8198	742.9842	2	19.12197	NA	NA	134.3119	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
SLA	OUM	-267.6317	543.2633	543.8267	4	27.8069	31.58456	27.69872	195.71415	NA	NA	1.437068	0.4857187
SLA	OU1	-269.1492	544.2984	544.6317	3	28.87285	NA	NA	172.49142	NA	NA	1.210615	0.5725577
SLA	BM	-308.74	621.48	621.6444	2	27.46633	NA	NA	27.21009	NA	NA	NA	NA
SLA	BMM	-308.5809	623.1617	623.4951	3	27.47859	NA	NA	NA	25.0383	28.19873	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
XMID	OUM	-189.7155	387.431	387.9944	4	-21.90274	-20.71753	-21.93775	917.23819	NA	NA	52.996002	0.2324302
XMID	OU1	-190.9815	387.9631	388.2964	3	-21.56552	NA	NA	27.333966	NA	NA	1.511488	0.4585861
XMID	BM	-221.5564	447.1128	447.2772	2	-21.14576	NA	NA	2.743632	NA	NA	NA	NA
XMID	BMM	-221.4093	448.8185	449.1518	3	-21.15394	NA	NA	NA	3.064349	2.636991	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
TOL_XMID	OUM	25.333455	-42.66691	-42.10353	4	0.001407006	0.1188104	-0.002156394	0.027398851	NA	NA	0.4127846	1.721991
TOL_XMID	OU1	23.203339	-40.406679	-40.073345	3	0.031016983	NA	NA	0.024686259	NA	NA	0.3444015	2.012614
TOL_XMID	BMM	8.067568	-10.135136	-9.801803	3	-0.004128193	NA	NA	NA	0.0103509	0.005457898	NA	NA

TOL_XMID	BM	6.352536	-8.705071	-8.540688	2	0.000952536	NA	NA	0.006817101	NA	NA	NA	NA

Sowing N. 2 (S2) - Stochastic map : ARD - Treatment : H

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
ASYM	OUM	-340.6925	689.3851	689.9485	4	44.10205	29.91723	66.45429	286.8854	NA	NA	0.266724	2.697017
ASYM	OU1	-347.6925	701.3851	701.7184	3	54.56125	NA	NA	190.852	NA	NA	0.1239679	5.591343
ASYM	BMM	-355.9237	717.8475	718.1808	3	50.46849	NA	NA	NA	42.86383	139.6617	NA	NA
ASYM	BM	-360.5413	725.0826	725.247	2	54.35073	NA	NA	106.3548	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
TOL_ASYM	OUM	-111.7894	231.5788	232.1422	4	0.1251074	-0.3015493	0.7855223	2.0198952	NA	NA	0.8769571	0.7988238
TOL_ASYM	OU1	-117.825	241.65	241.9833	3	0.4335541	NA	NA	1.7958177	NA	NA	0.6534058	1.0608219
TOL_ASYM	BMM	-146.9782	299.9565	300.2898	3	0.2326191	NA	NA	NA	0.1787778	0.5678292	NA	NA
TOL_ASYM	BM	-152.2036	308.4072	308.5716	2	0.3895452	NA	NA	0.4422895	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
IGR	OU1	99.52526	-193.0505	-192.7172	3	0.5766931	NA	NA	0.216769455	NA	NA	25.4035	0.0272855
IGR	OUM	99.53132	-191.0626	-190.4993	4	0.5763471	0.5760289	0.5770062	0.202570028	NA	NA	23.74124	0.03262778
IGR	BM	54.72913	-105.4583	-105.2939	2	0.5738896	NA	NA	0.001908592	NA	NA	NA	NA
IGR	BMM	54.8906	-103.7812	-103.4479	3	0.5738791	NA	NA	NA	0.001899018	0.001939048	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
TOL_IGR	OU1	27.753	-49.50599	-49.17266	3	0.02170286	NA	NA	1.25163397	NA	NA	22.18821	0.03123944
TOL_IGR	OUM	27.78119	-47.56238	-46.999	4	0.02424637	0.02823625	0.01870061	4.49814194	NA	NA	79.79329	0.0251726
TOL_IGR	BMM	-32.9356	71.8712	72.20454	3	0.02774738	NA	NA	NA	0.009277395	0.02775157	NA	NA
TOL_IGR	BM	-38.04107	80.08214	80.24653	2	0.03537018	NA	NA	0.02192631	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
LA	OUM	-553.4361	1114.872	1115.436	4	360.2697	183.6408	627.1045	121149.59	NA	NA	0.445351	1.816702
LA	BMM	-555.8928	1117.786	1118.119	3	419.943	NA	NA	NA	1979.875	44675.51	NA	NA
LA	OU1	-558.8595	1123.719	1124.052	3	498.3898	NA	NA	61703.51	NA	NA	0.168527	4.112973
LA	BM	-573.506	1151.012	1151.176	2	538.2755	NA	NA	28886.09	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
LDI	OUM	-57.63234	123.2647	123.8281	4	1.788496	1.601159	2.080454	0.10025394	NA	NA	0.1394308	5.003872
LDI	OU1	-59.22021	124.4404	124.7738	3	1.912012	NA	NA	0.08980137	NA	NA	0.1115596	6.213245
LDI	BMM	-67.21549	140.431	140.7643	3	1.903483	NA	NA	NA	0.03001319	0.06053214	NA	NA
LDI	BM	-69.28806	142.5761	142.7405	2	1.947489	NA	NA	0.04989777	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
LDMC	OUM	-204.7781	417.5561	418.1195	4	14.15253	12.72004	16.23212	13.3057	NA	NA	0.4755696	1.581337
LDMC	OU1	-208.9601	423.9201	424.2534	3	15.14738	NA	NA	8.796182	NA	NA	0.261853	2.647085
LDMC	BMM	-219.2929	444.5858	444.9192	3	15.03841	NA	NA	NA	1.079072	3.97023	NA	NA
LDMC	BM	-224.4446	452.8892	453.0536	2	15.45651	NA	NA	2.960294	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
LTH	OU1	112.18552	-218.371	-218.0377	3	0.2675458	NA	NA	0.130723191	NA	NA	21.37728	0.03242448
LTH	OUM	112.2122	-216.4244	-215.861	4	0.2688633	0.2709128	0.2658397	0.109200831	NA	NA	17.85326	0.18685209
LTH	BMM	69.80782	-133.6156	-133.2823	3	0.2647906	NA	NA	NA	0.000893986	0.001581821	NA	NA
LTH	BM	68.25048	-132.501	-132.3366	2	0.2626811	NA	NA	0.001337151	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
MGR	OU1	-45.67195	97.34389	97.67723	3	0.6541839	NA	NA	0.28128003	NA	NA	0.6858438	1.0106488
MGR	OUM	-44.87783	97.75567	98.31905	4	0.6967027	0.759261	0.6041876	0.28452511	NA	NA	0.7100479	0.9783952
MGR	BMM	-63.92869	133.85739	134.19072	3	0.6117796	NA	NA	NA	0.106819	0.02458706	NA	NA
MGR	BM	-73.12527	150.25054	150.41493	2	0.6575898	NA	NA	0.05519959	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
TOL_MGR	OUM	-155.3046	318.6092	319.1726	4	2.069523	2.427414	1.518578	6.089636	NA	NA	0.8399487	0.8293756
TOL_MGR	OU1	-156.8123	319.6247	319.958	3	1.811094	NA	NA	5.910326	NA	NA	0.7802977	0.8883112
TOL_MGR	BMM	-176.4896	358.9791	359.3124	3	1.599637	NA	NA	NA	2.032109	0.4777623	NA	NA
TOL_MGR	BM	-186.2489	376.4978	376.6622	2	1.82147	NA	NA	1.083437	NA	NA	NA	NA

Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
NLEA	OU1	-282.5824	571.1648	571.4981	3	14.45613	NA	NA	32.85245	NA	NA	0.1157572	5.987942
NLEA	OUM	-282.3251	572.6502	573.2136	4	13.52717	12.49351	15.6367	32.56975	NA	NA	0.1154221	6.006866
NLEA	BMM	-287.6465	581.293	581.6263	3	13.00926	NA	NA	NA	11.54503	18.83729	NA	NA
NLEA	BM	-289.0769	582.1538	582.3182	2	13.22124	NA	NA	16.21827	NA	NA	NA	NA

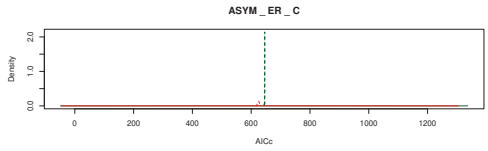
Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
RESpT2	OU1	-306.708	619.4161	619.7494	3	19.94326	NA	NA	3428.6116	NA	NA	9.146282	0.07578458
RESpT2	OUM	-305.6938	619.3877	619.9511	4	21.34689	23.24017	18.39221	25086.421	NA	NA	68.633049	0.06446781
RESpT2	BMM	-363.4196	732.8392	733.1725	3	19.27644	NA	NA	NA	50.70869	172.2017	NA	NA
RESpT2	BM	-369.4099	742.8198	742.9842	2	19.12197	NA	NA	134.3119	NA	NA	NA	NA

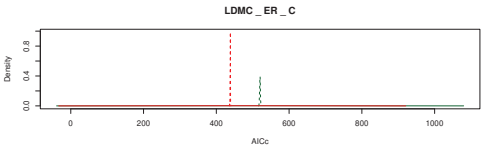
Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
SLA	OUM	-267.6093	543.2186	543.7819	4	30.00803	31.53811	27.65466	192.35942	NA	NA	1.41231	0.4946922
SLA	OU1	-269.1492	544.2984	544.6317	3	28.87285	NA	NA	172.49142	NA	NA	1.210615	0.5725577
SLA	BM	-308.74	621.48	621.6444	2	27.46633	NA	NA	27.21009	NA	NA	NA	NA
SLA	BMM	-307.8129	621.6258	621.9591	3	27.53275	NA	NA	NA	20.76219	30.79171	NA	NA

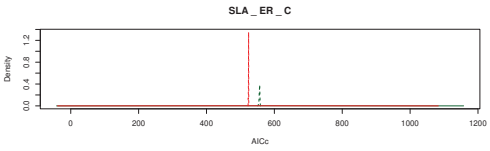
Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
XMID	OUM	-189.7757	387.5514	388.1148	4	-21.21543	-20.75117	-21.93108	1163.593826	NA	NA	67.236458	0.1652493
XMID	OU1	-190.9815	387.9631	388.2964	3	-21.56552	NA	NA	27.333966	NA	NA	1.511488	0.4585861
XMID	BM	-221.5564	447.1128	447.2772	2	-21.14576	NA	NA	2.743632	NA	NA	NA	NA
XMID	BMM	-221.2825	448.5649	448.8983	3	-21.14306	NA	NA	NA	2.517513	2.903757	NA	NA

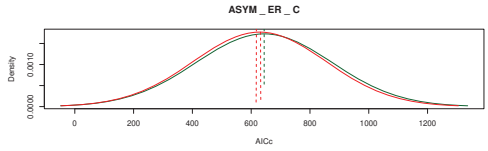
Result	model	LogLik	AIC	AICc	num_params	root_theta0	theta_high	theta_low	sigma	sigma_high	sigma_low	alpha	half_life
TOL_XMID	OUM	25.118763	-42.237525	-41.674145	4	0.06267707	0.1079077	-0.003397606	0.02686659	NA	NA	0.4014192	1.750819
TOL_XMID	OU1	23.203339	-40.406679	-40.073345	3	0.031016983	NA	NA	0.024686259	NA	NA	0.3444015	2.012614
TOL_XMID	BM	6.352536	-8.705071	-8.540688	2	0.000952536	NA	NA	0.006817101	NA	NA	NA	NA
TOL_XMID	BMM	7.016348	-8.032696	-7.699363	3	-0.003539351	NA	NA	NA	0.008481318	0.005954775	NA	NA

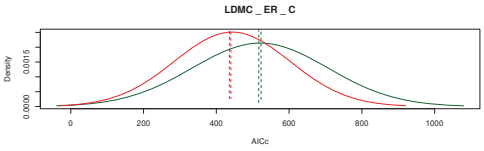
Supplementary material - A4 (Chapter 1)

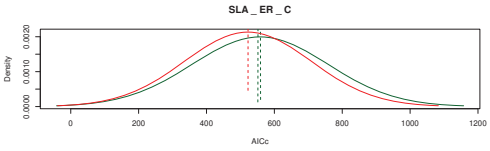


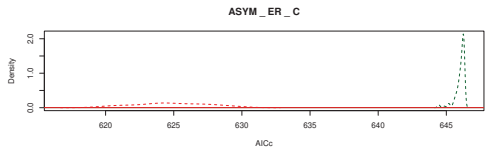


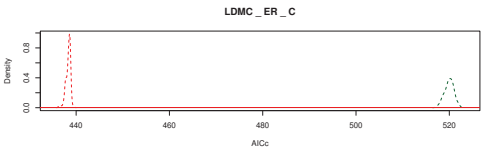


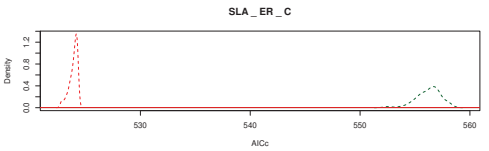


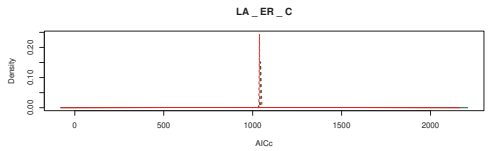


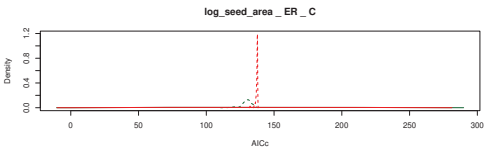


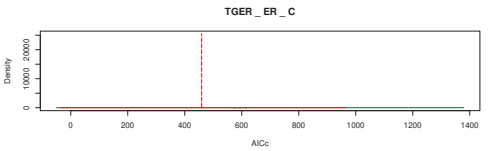


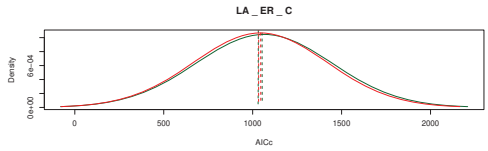


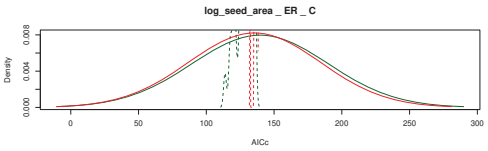


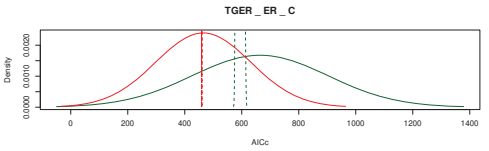


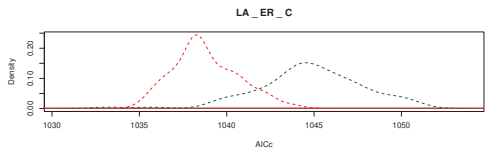


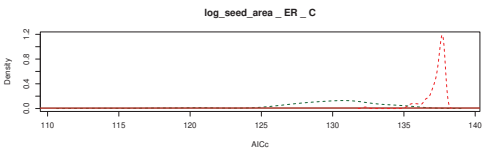


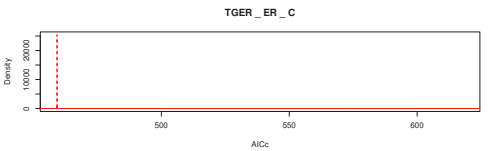


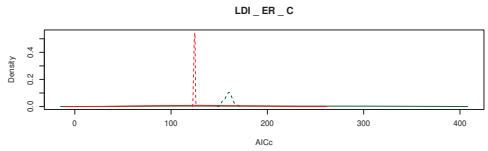


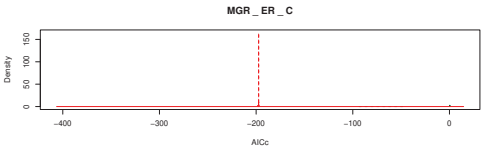


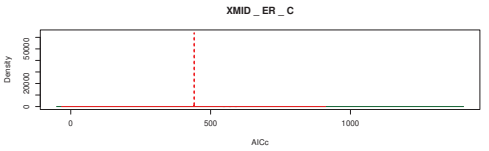


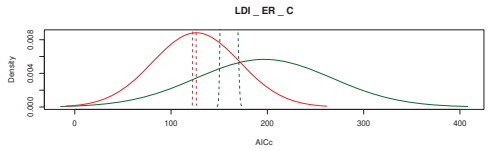


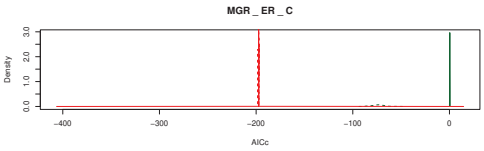


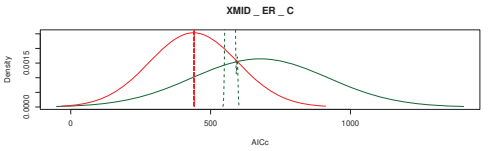


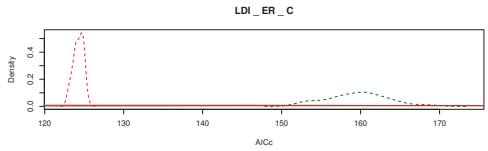


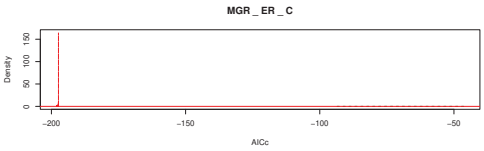


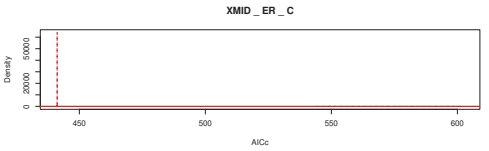


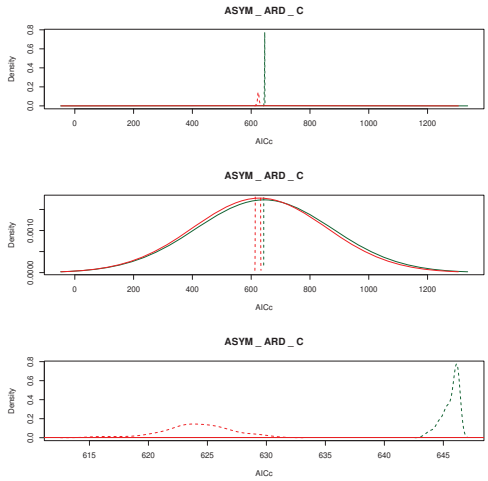


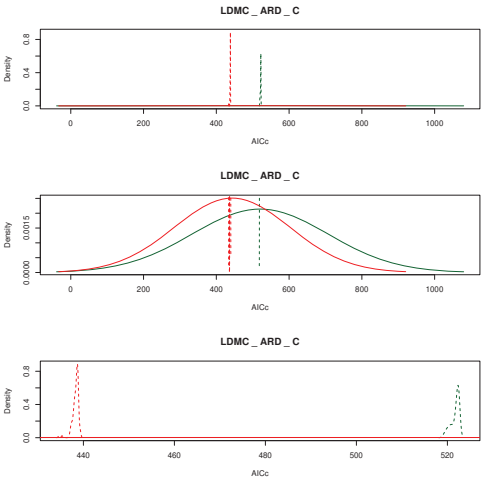


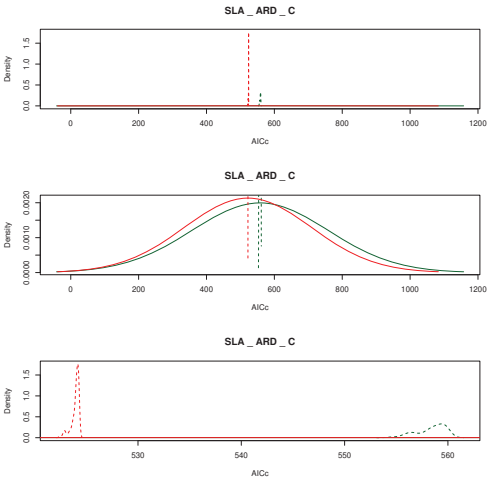







ASYM _ ARD _ C
Density
AICc

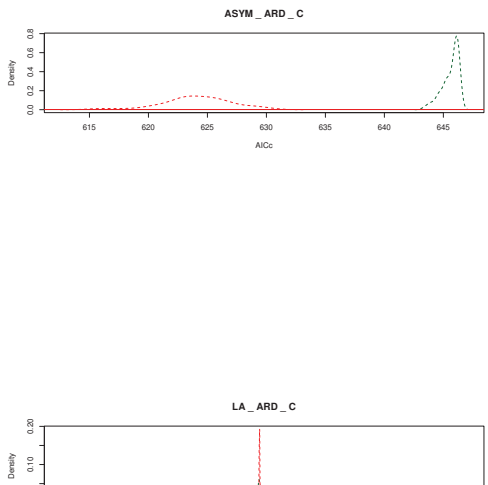

LDMC _ ARD _ C
Density
AICc

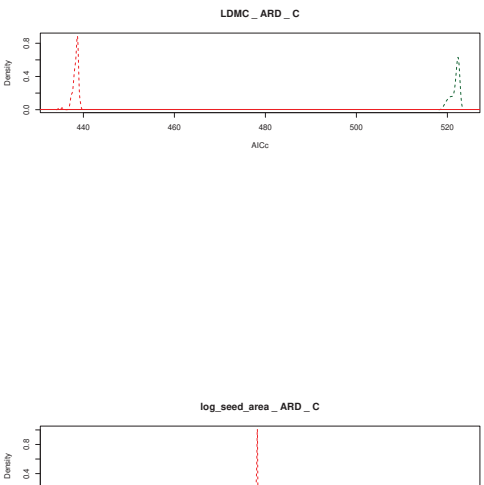

SLA _ ARD _ C
Density
AICc

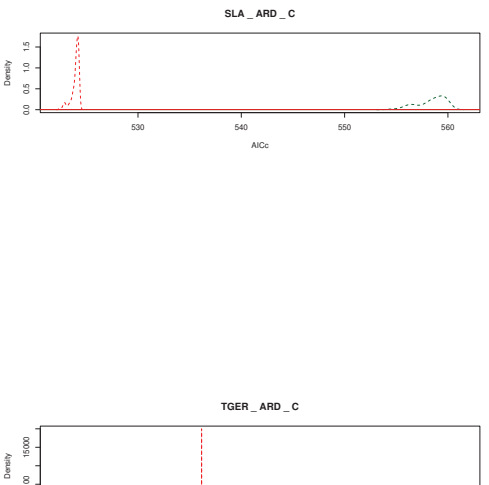
ASYM _ ARD _ C
Density
AICc

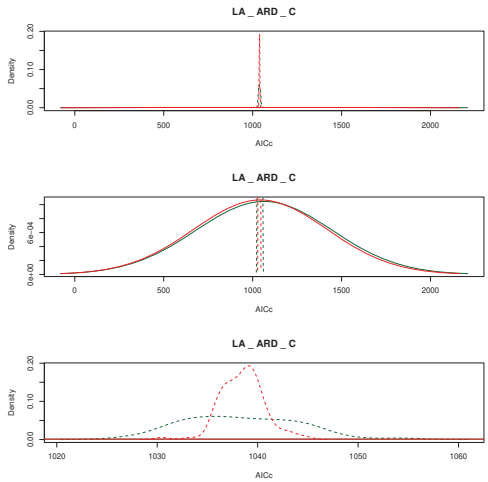
LDMC _ ARD _ C
Density
AICc

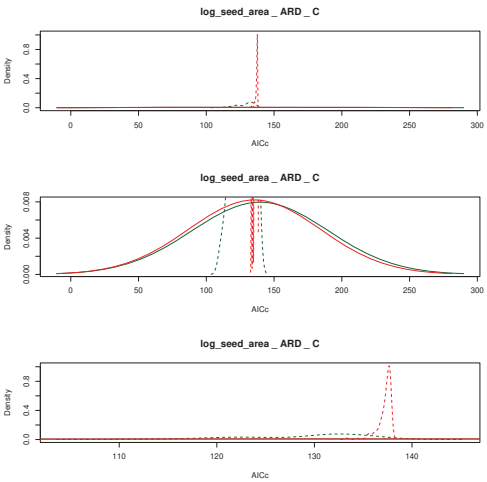
SLA _ ARD _ C
Density
AICc

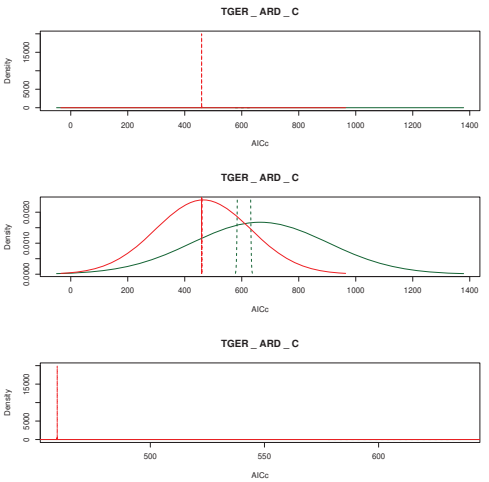

ASYM _ ARD _ C
Density
AICc


LDMC _ ARD _ C
Density
AICc


SLA _ ARD _ C
Density
AICc


LA _ ARD _ C
Density
AICc

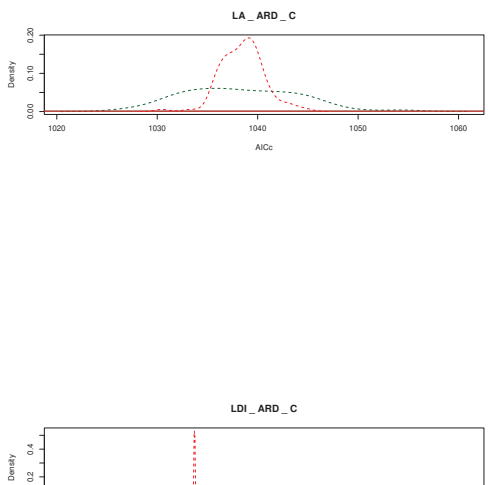

log_seed_area _ ARD _ C
Density
AICc

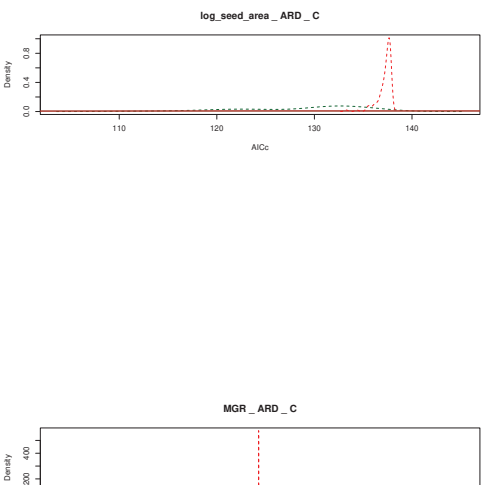

TGER _ ARD _ C
Density
AICc

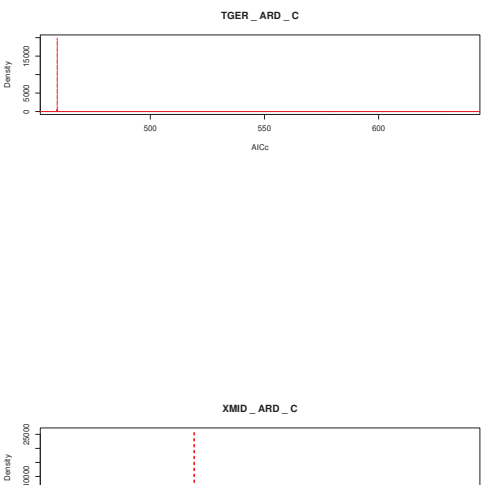
LA _ ARD _ C
Density
AICc

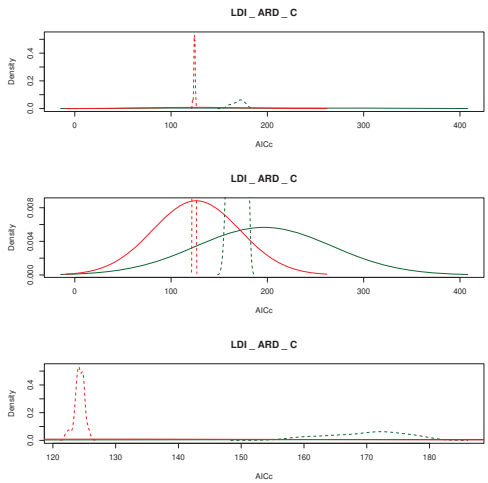
log_seed_area _ ARD _ C
Density
AICc

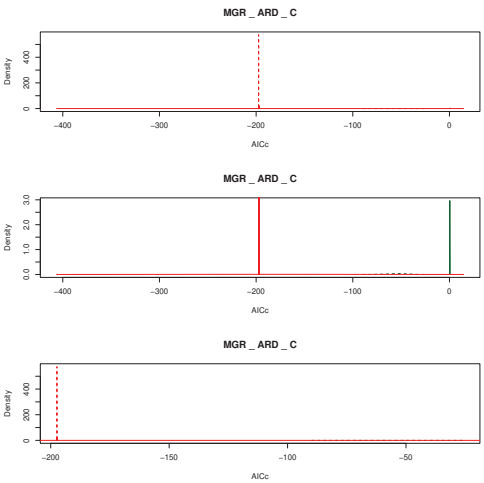
TGER _ ARD _ C
Density
AICc

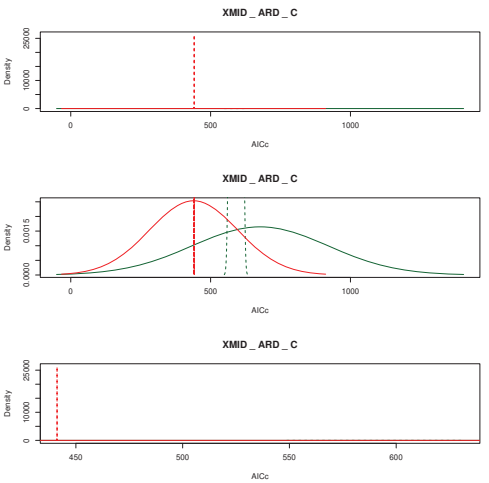

LA _ ARD _ C
Density
AICc


log_seed_area _ ARD _ C
Density
AICc


TGER _ ARD _ C
Density
AICc


LDI _ ARD _ C
Density
AICc


MGR _ ARD _ C
Density
AICc


XMID _ ARD _ C
Density
AICc

LDI _ ARD _ C
Density
AICc

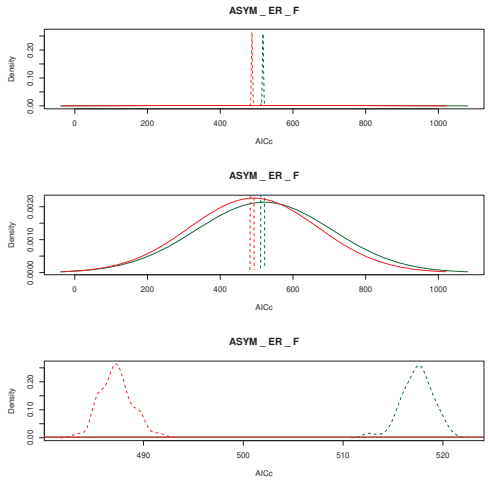
MGR _ ARD _ C
Density
AICc

XMID _ ARD _ C
Density
AICc

LDI _ ARD _ C
Density
AICc

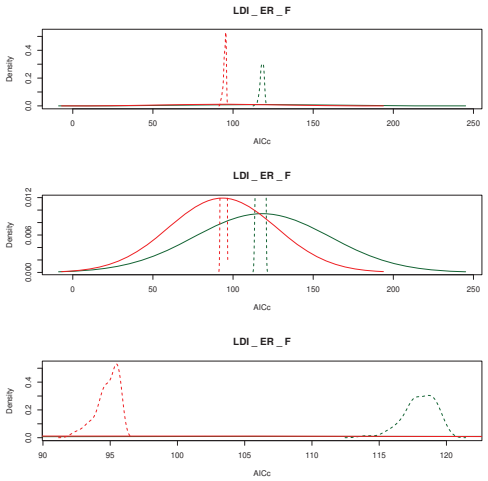
MGR _ ARD _ C
Density
AICc

XMID _ ARD _ C
Density
AICc


ASYM _ ER _ F
Density
AICc

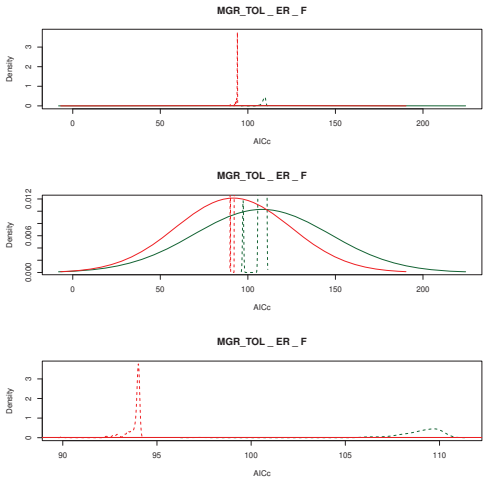
ASYM _ ER _ F
Density
AICc

ASYM _ ER _ F
Density
AICc


LDI _ ER _ F
Density
AICc

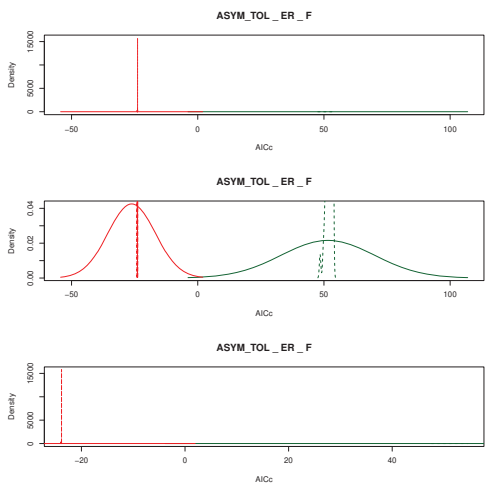
LDI _ ER _ F
Density
AICc

LDI _ ER _ F
Density
AICc


MGR_TOL _ ER _ F
Density
AICc

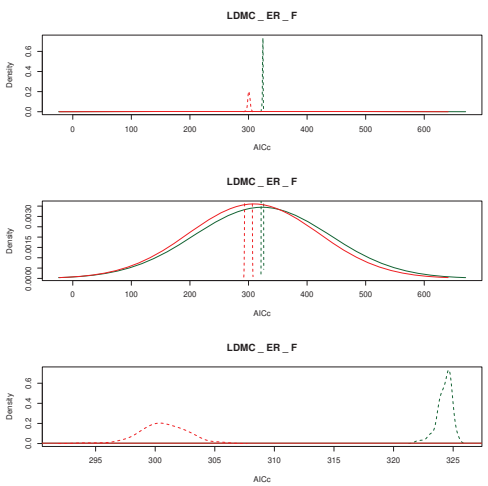
MGR_TOL _ ER _ F
Density
AICc

MGR_TOL _ ER _ F
Density
AICc


ASYM_TOL _ ER _ F
Density
AICc

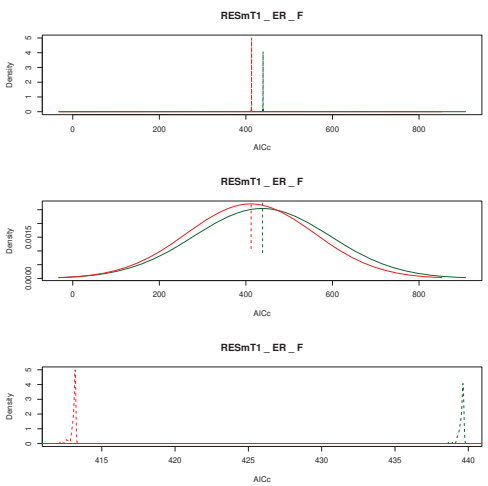
ASYM_TOL _ ER _ F
Density
AICc

ASYM_TOL _ ER _ F
Density
AICc


LDMC _ ER _ F
Density
AICc

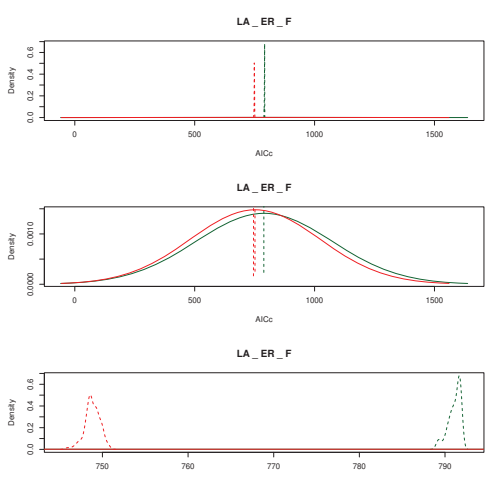
LDMC _ ER _ F
Density
AICc

LDMC _ ER _ F
Density
AICc


RESmT1 _ ER _ F
Density
AICc

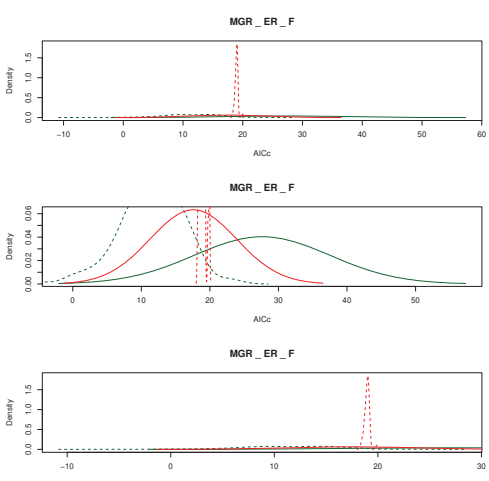
RESmT1 _ ER _ F
Density
AICc

RESmT1 _ ER _ F
Density
AICc


LA _ ER _ F
Density
AICc

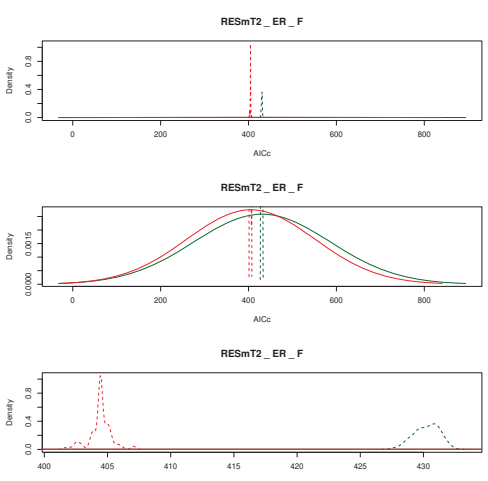
LA _ ER _ F
Density
AICc

LA _ ER _ F
Density
AICc


MGR _ ER _ F
Density
AICc

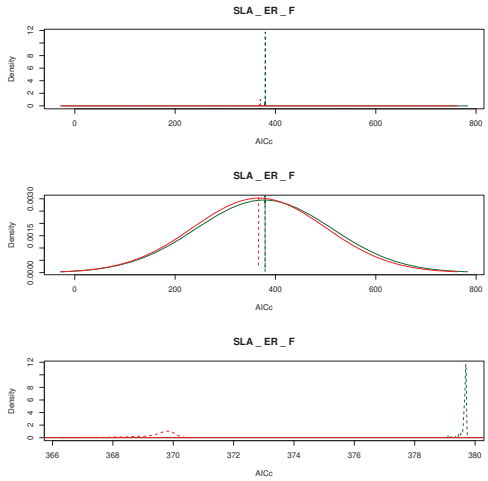
MGR _ ER _ F
Density
AICc

MGR _ ER _ F
Density
AICc


RESmT2 _ ER _ F
Density
AICc

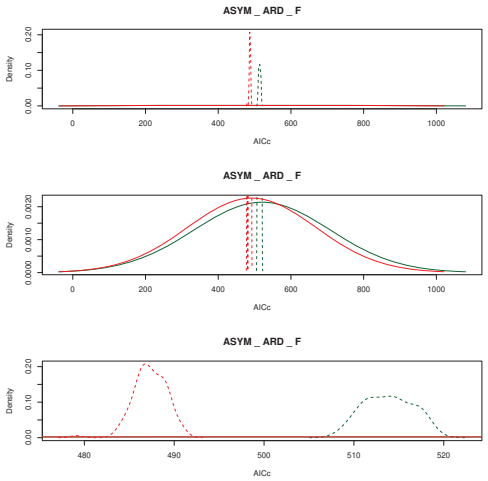
RESmT2 _ ER _ F
Density
AICc

RESmT2 _ ER _ F
Density
AICc


SLA _ ER _ F
Density
AICc

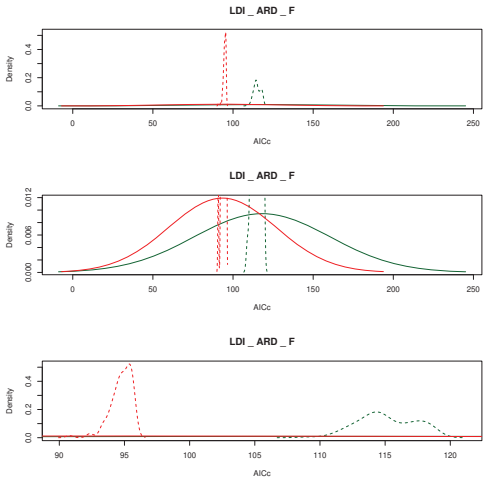
SLA _ ER _ F
Density
AICc

SLA _ ER _ F
Density
AICc


ASYM _ ARD _ F
Density
AICc

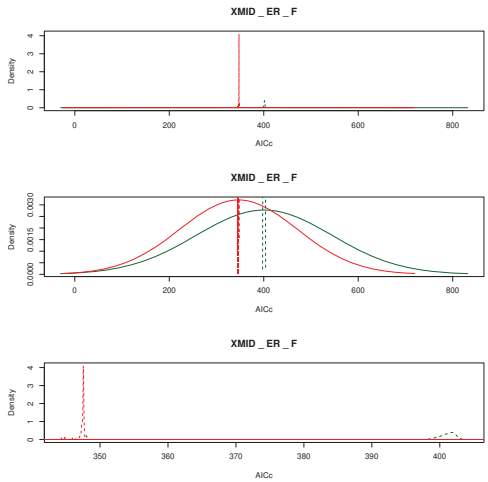
ASYM _ ARD _ F
Density
AICc

ASYM _ ARD _ F
Density
AICc


LDI _ ARD _ F
Density
AICc

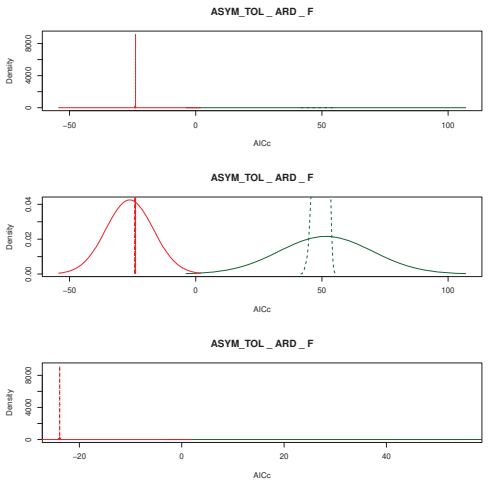
LDI _ ARD _ F
Density
AICc

LDI _ ARD _ F
Density
AICc


XMID _ ER _ F
Density
AICc

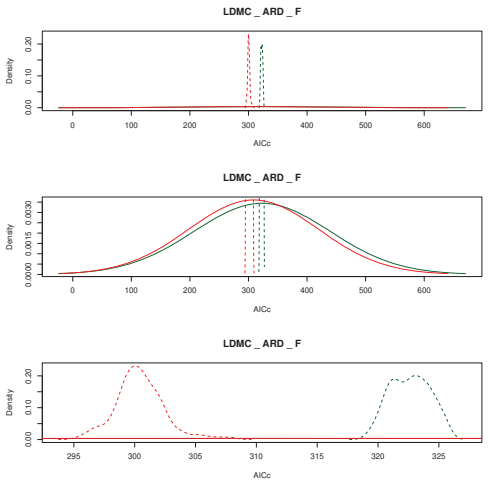
XMID _ ER _ F
Density
AICc

XMID _ ER _ F
Density
AICc


ASYM_TOL _ ARD _ F
Density
AICc

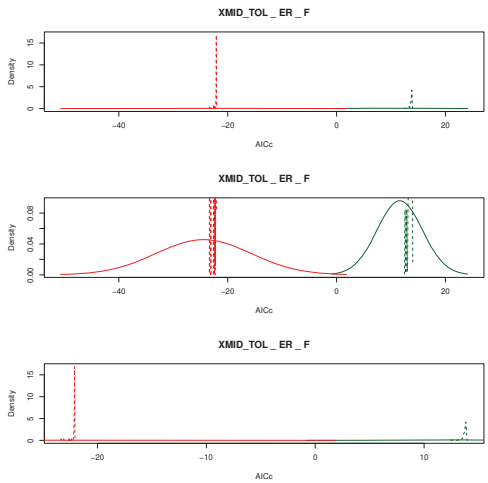
ASYM_TOL _ ARD _ F
Density
AICc

ASYM_TOL _ ARD _ F
Density
AICc


LDMC _ ARD _ F
Density
AICc

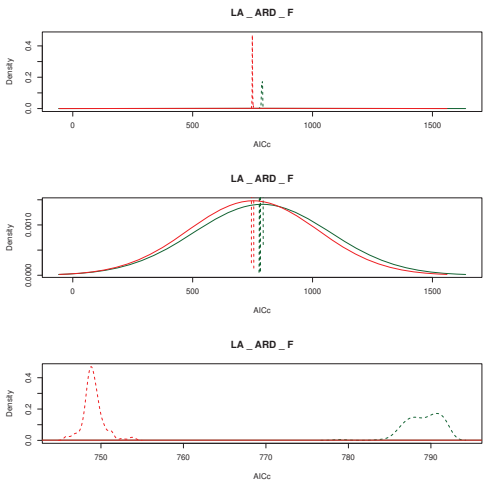
LDMC _ ARD _ F
Density
AICc

LDMC _ ARD _ F
Density
AICc


XMID_TOL _ ER _ F
Density
AICc

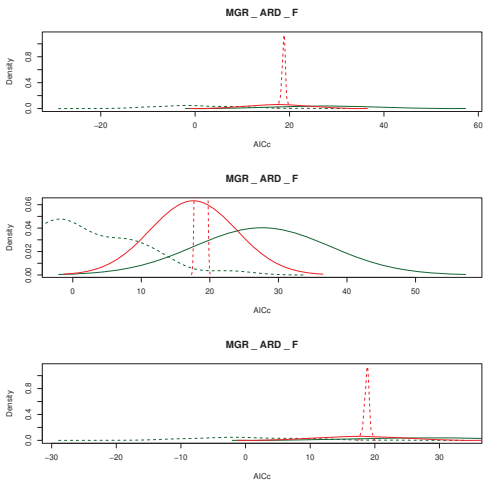
XMID_TOL _ ER _ F
Density
AICc

XMID_TOL _ ER _ F
Density
AICc


LA _ ARD _ F
Density
AICc

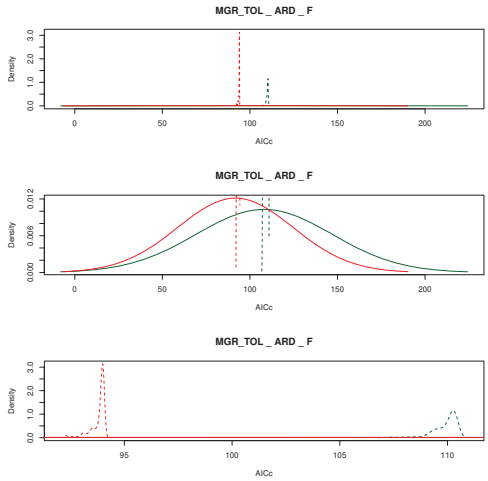
LA _ ARD _ F
Density
AICc

LA _ ARD _ F
Density
AICc


MGR _ ARD _ F
Density
AICc

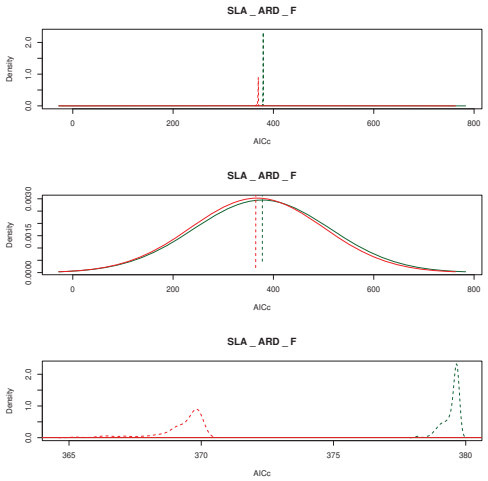
MGR _ ARD _ F
Density
AICc

MGR _ ARD _ F
Density
AICc


MGR_TOL _ ARD _ F
Density
AICc

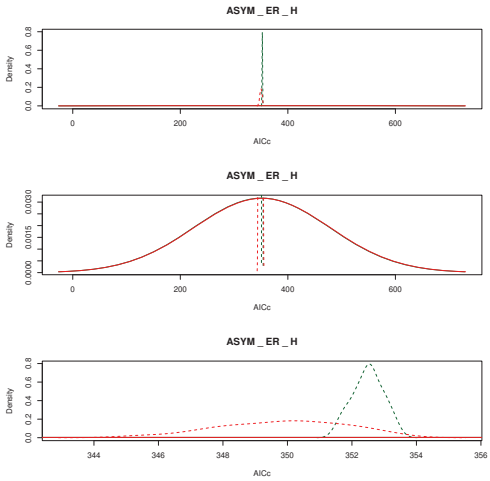
MGR_TOL _ ARD _ F
Density
AICc

MGR_TOL _ ARD _ F
Density
AICc


SLA _ ARD _ F
Density
AICc

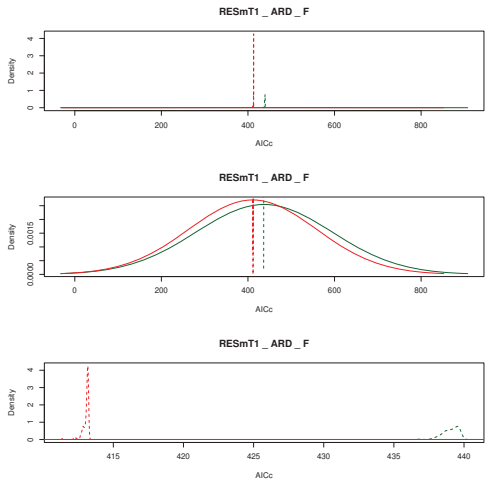
SLA _ ARD _ F
Density
AICc

SLA _ ARD _ F
Density
AICc


ASYM _ ER _ H
Density
AICc

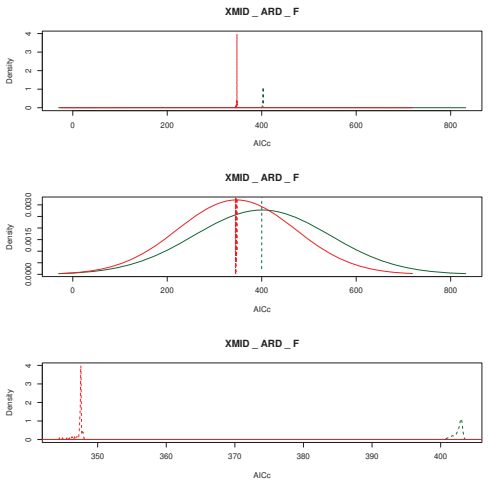
ASYM _ ER _ H
Density
AICc

ASYM _ ER _ H
Density
AICc


RESmT1 _ ARD _ F
Density
AICc

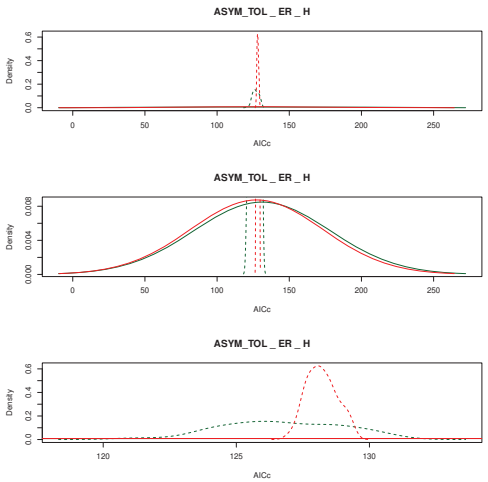
RESmT1 _ ARD _ F
Density
AICc

RESmT1 _ ARD _ F
Density
AICc


XMID _ ARD _ F
Density
AICc

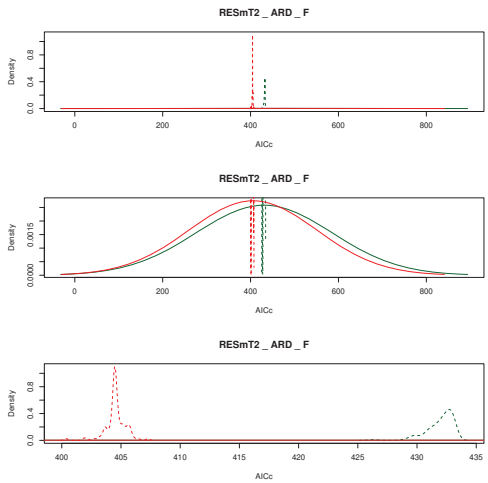
XMID _ ARD _ F
Density
AICc

XMID _ ARD _ F
Density
AICc


ASYM_TOL _ ER _ H
Density
AICc

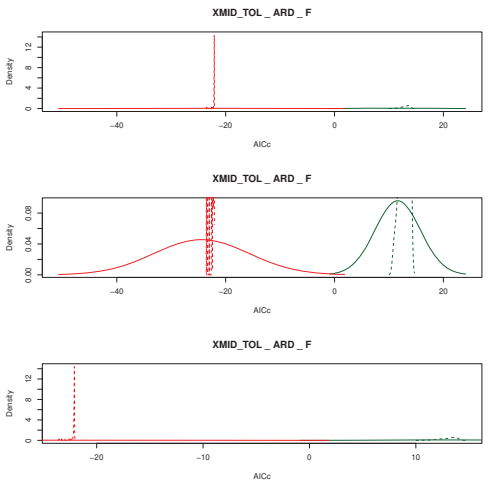
ASYM_TOL _ ER _ H
Density
AICc

ASYM_TOL _ ER _ H
Density
AICc


RESmT2 _ ARD _ F
Density
AICc

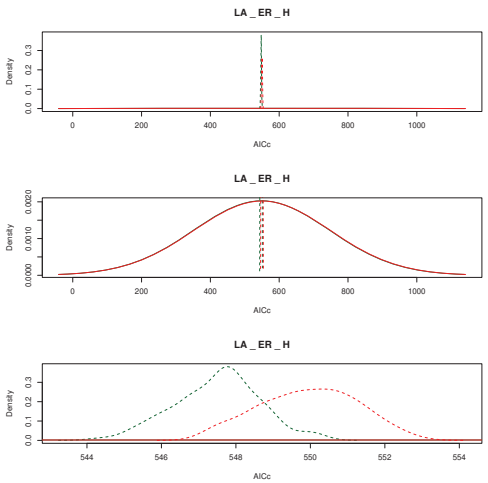
RESmT2 _ ARD _ F
Density
AICc

RESmT2 _ ARD _ F
Density
AICc


XMID_TOL _ ARD _ F
Density
AICc

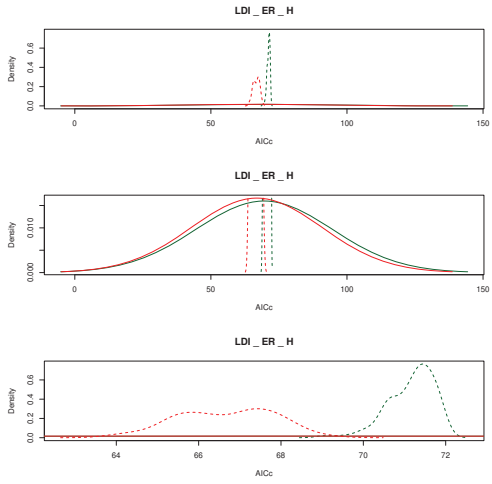
XMID_TOL _ ARD _ F
Density
AICc

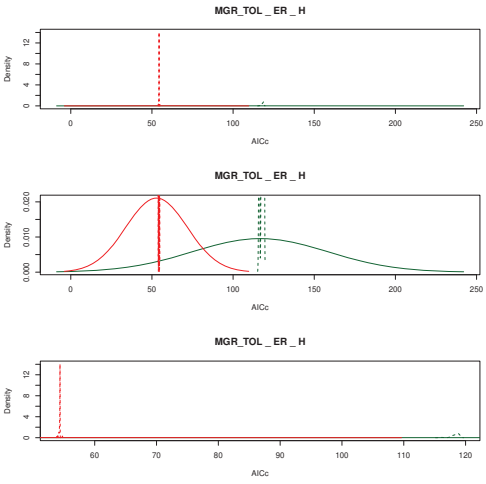
XMID_TOL _ ARD _ F
Density
AICc

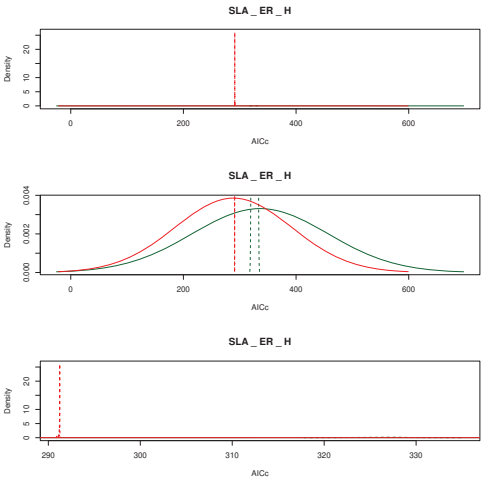

LA _ ER _ H
Density
AICc

LA _ ER _ H
Density
AICc

LA _ ER _ H
Density
AICc


LDI _ ER _ H
Density
AICc


MGR_TOL _ ER _ H
Density
AICc


SLA _ ER _ H
Density
AICc

LDI _ ER _ H
Density
AICc

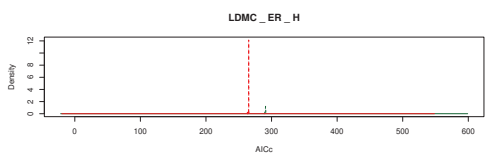
MGR_TOL _ ER _ H
Density
AICc

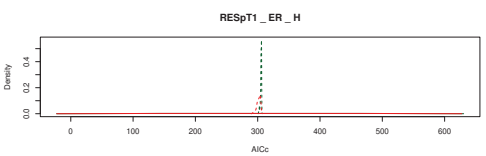
SLA _ ER _ H
Density
AICc

LDI _ ER _ H
Density
AICc

MGR_TOL _ ER _ H
Density
AICc

SLA _ ER _ H
Density
AICc


LDMC _ ER _ H
Density
AICc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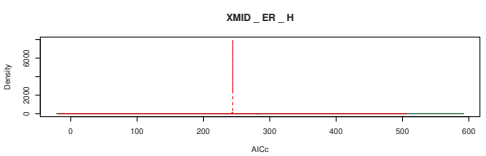
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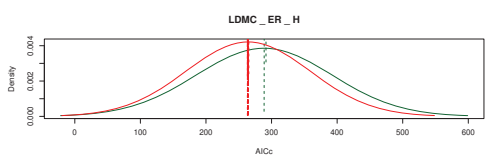
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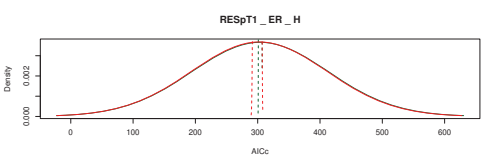
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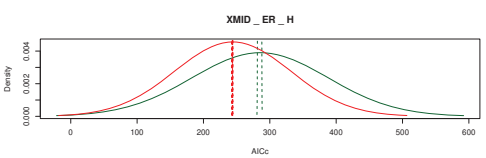
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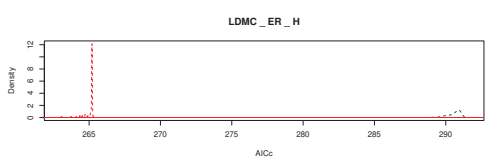
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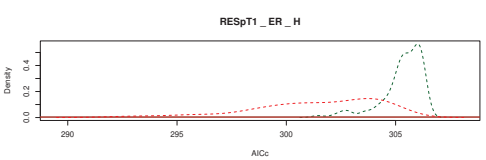
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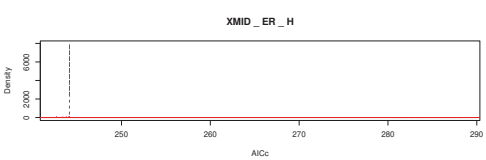
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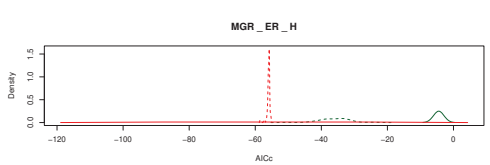
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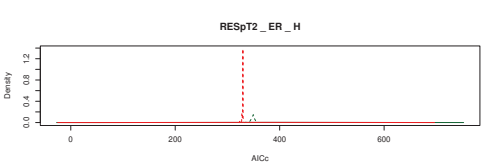
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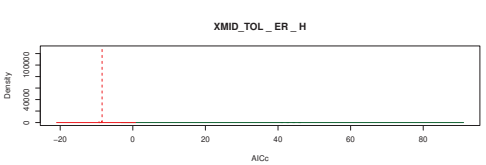
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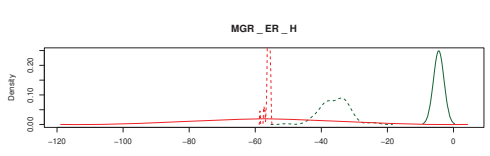
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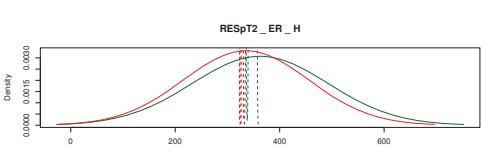
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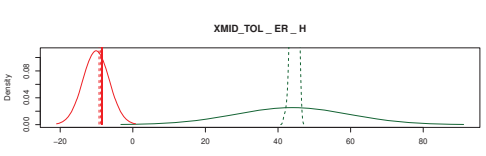
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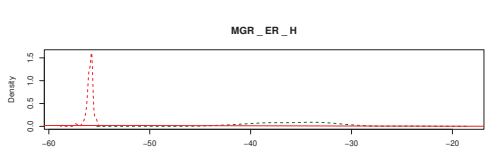
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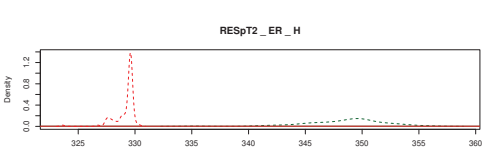
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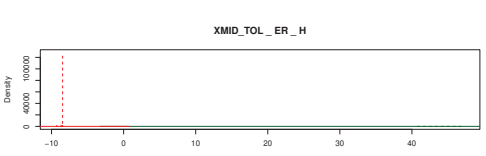
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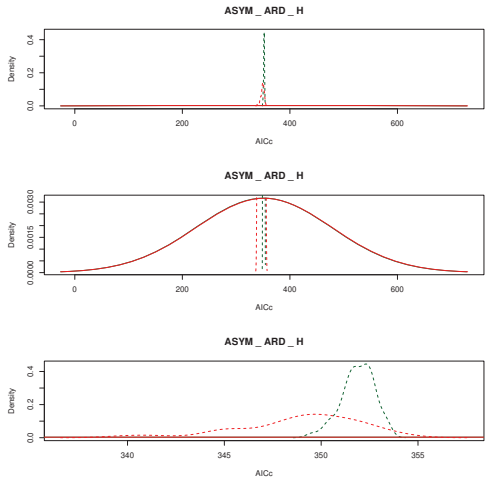
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Density
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ASYM _ ARD _ H
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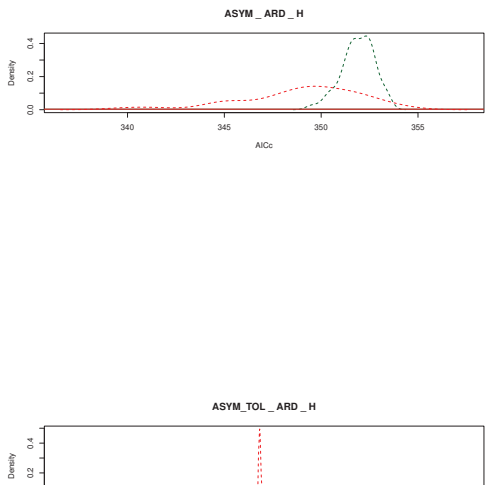
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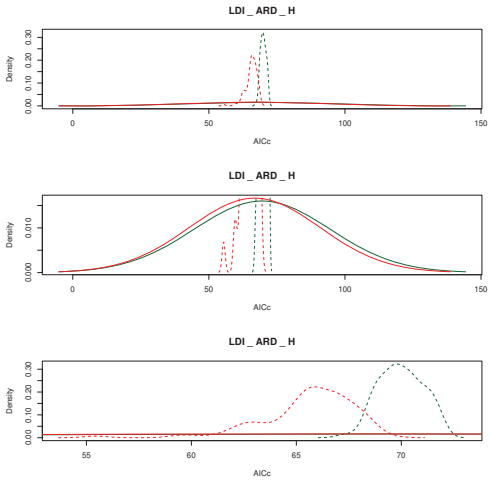
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Density
AICc

LDI _ ARD _ H
Density
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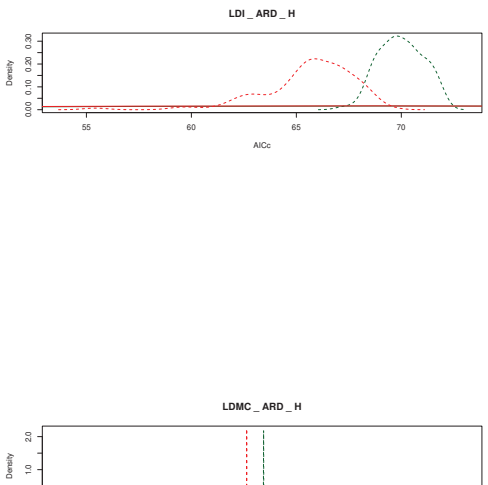
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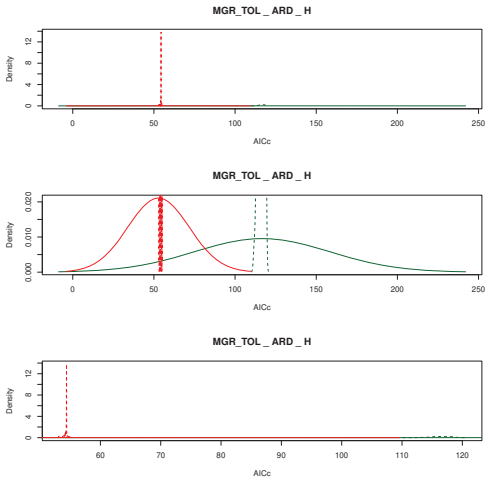
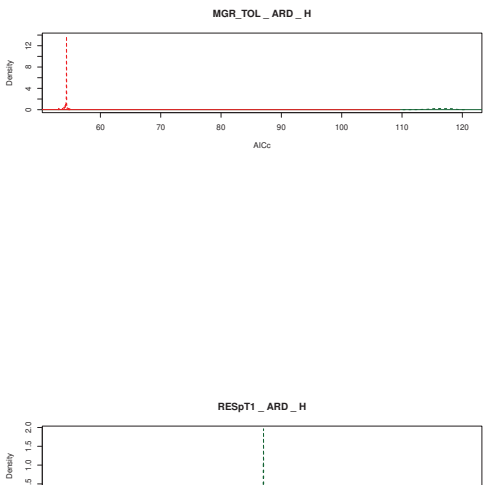

MGR_TOL _ ARD _ H
Density
AICc

MGR_TOL _ ARD _ H
Density
AICc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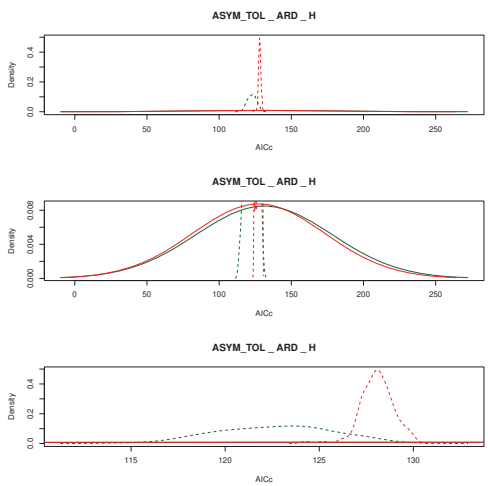
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Density
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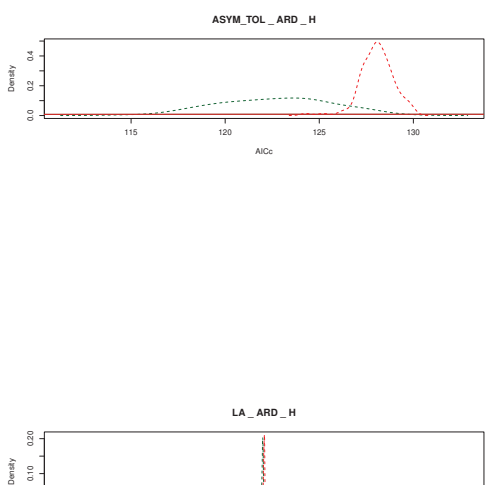
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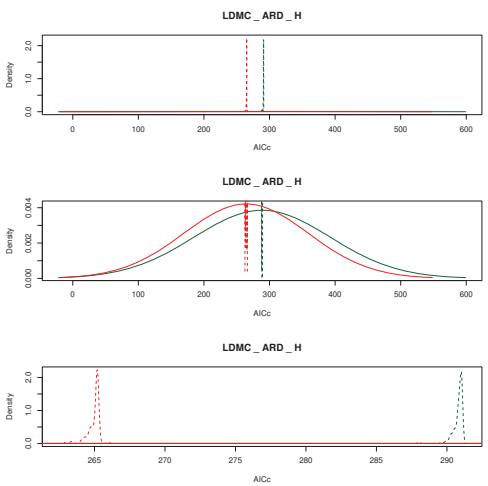
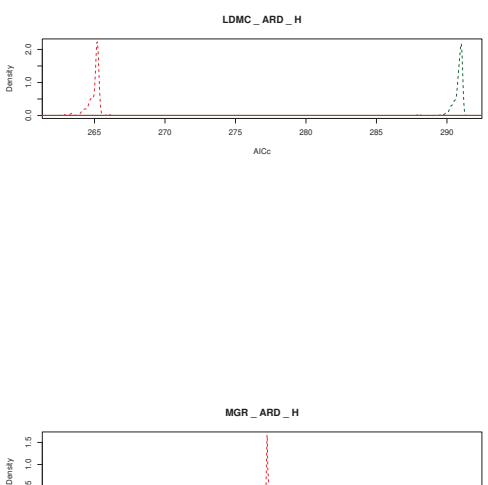
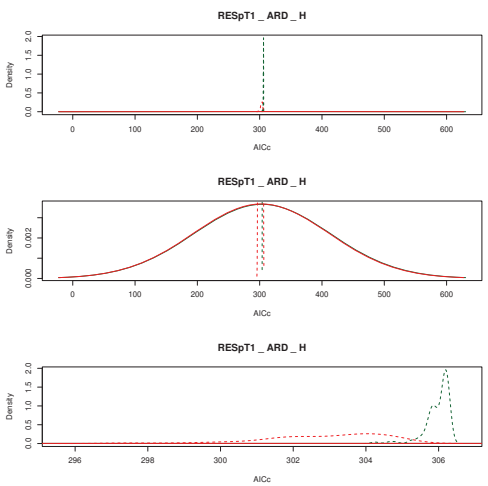
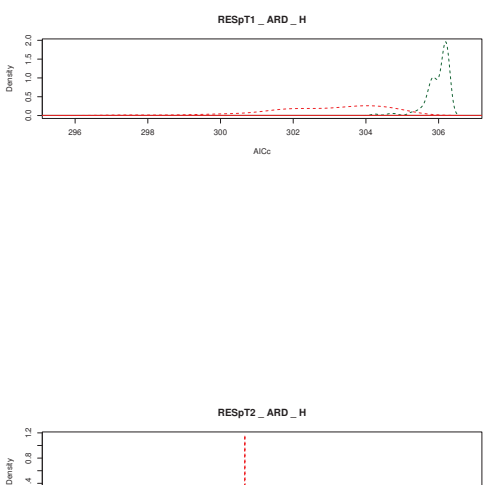

LDMC _ ARD _ H
Density
AICc

LDMC _ ARD _ H
Density
AICc


LDMC _ ARD _ H
Density
AICc


RESpT1 _ ARD _ H
Density
AICc

RESpT1 _ ARD _ H
Density
AICc


RESpT1 _ ARD _ H
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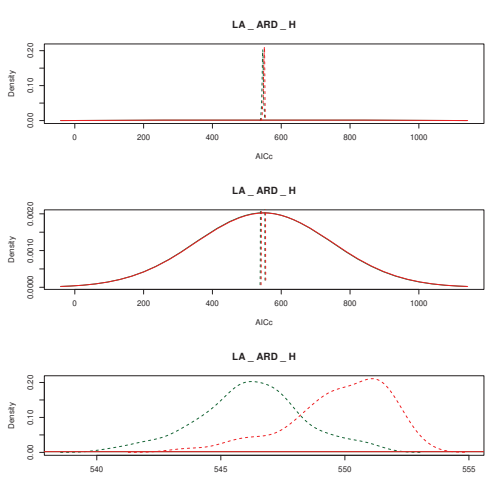
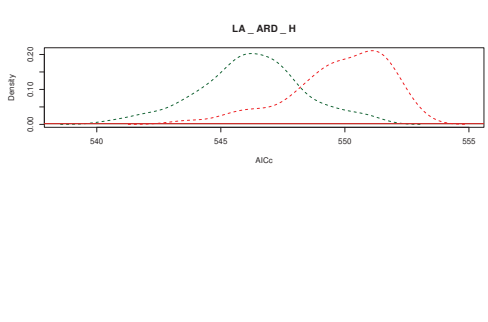

LA _ ARD _ H
Density
AICc

LA _ ARD _ H
Density
AICc


LA _ ARD _ H
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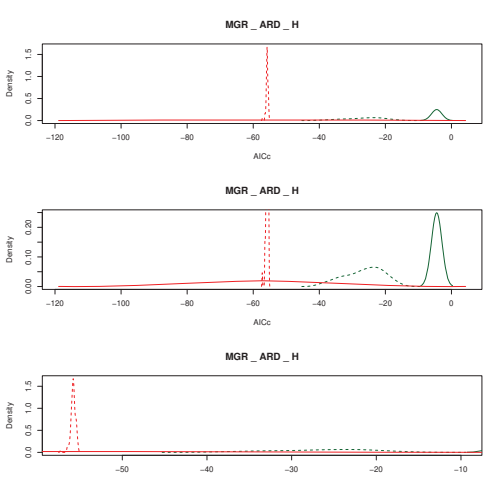
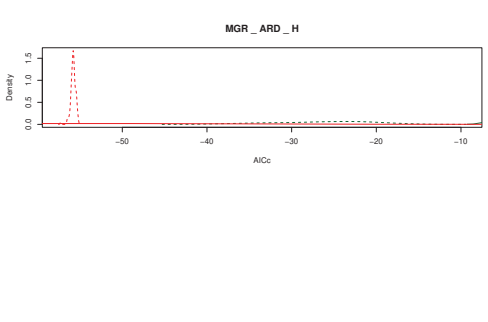

MGR _ ARD _ H
Density
AICc

MGR _ ARD _ H
Density
AICc


MGR _ ARD _ H
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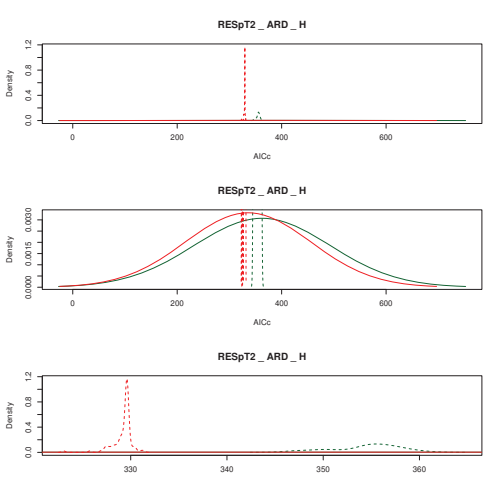
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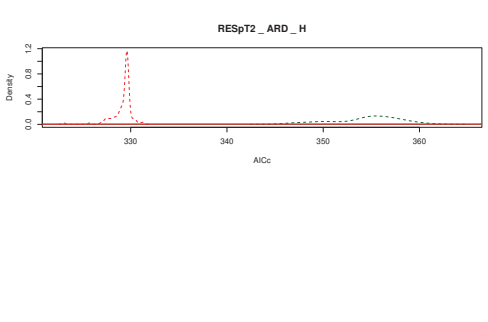
AICc

RESpT2 _ ARD _ H
Density
AICc


RESpT2 _ ARD _ H
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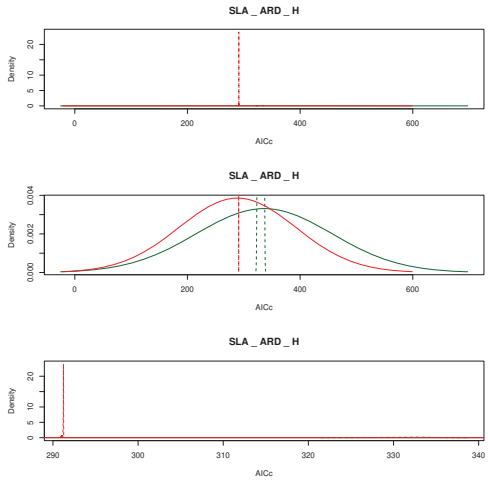
SLA _ ARD _ H
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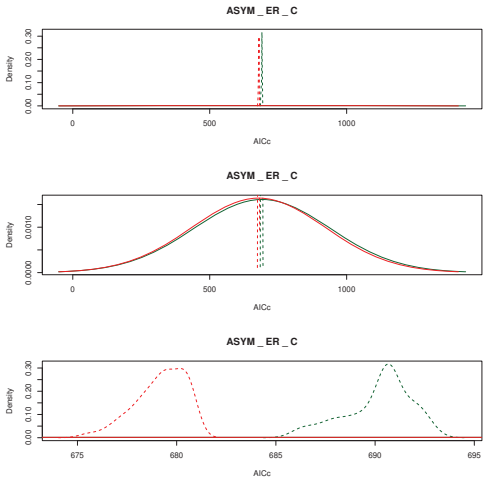
SLA _ ARD _ H
Density
AICc

SLA _ ARD _ H
Density
AICc


ASYM _ ER _ C
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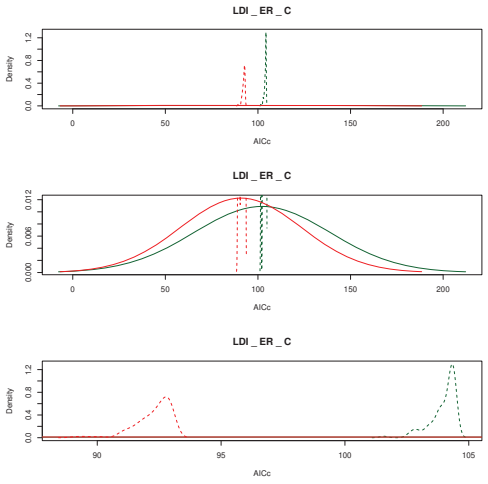
AICc

ASYM _ ER _ C
Density
AICc

ASYM _ ER _ C
Density
AICc


LDI _ ER _ C
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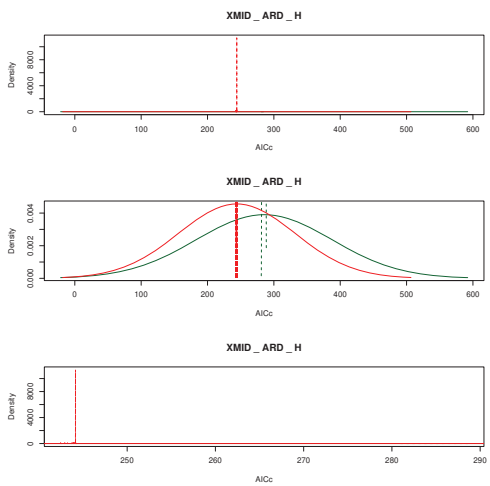
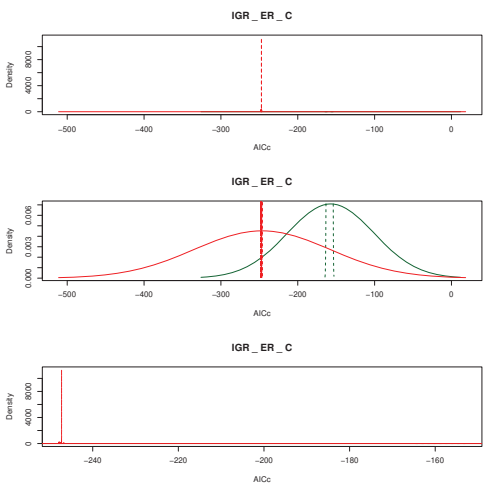
LDI _ ER _ C
Density
AICc

LDI _ ER _ C
Density
AICc


XMID _ ARD _ H
Density
AICc

XMID _ ARD _ H
Density
AICc

XMID _ ARD _ H
Density
AICc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IGR _ ER _ C
Density
AICc

IGR _ ER _ C
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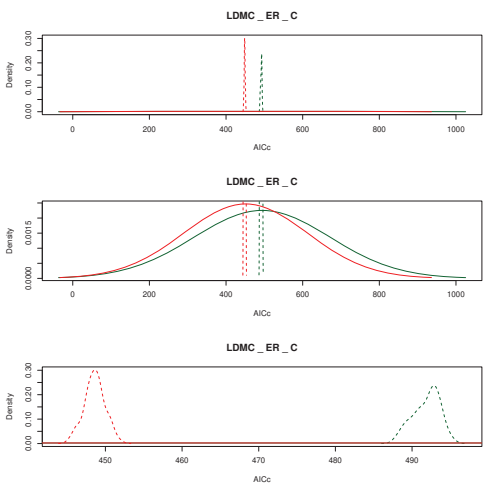
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LDMC _ ER _ C
Density
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LDMC _ ER _ C
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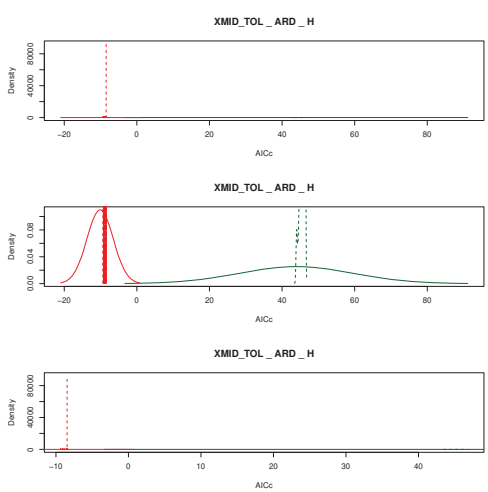
XMID_TOL _ ARD _ H
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XMID_TOL _ ARD _ H
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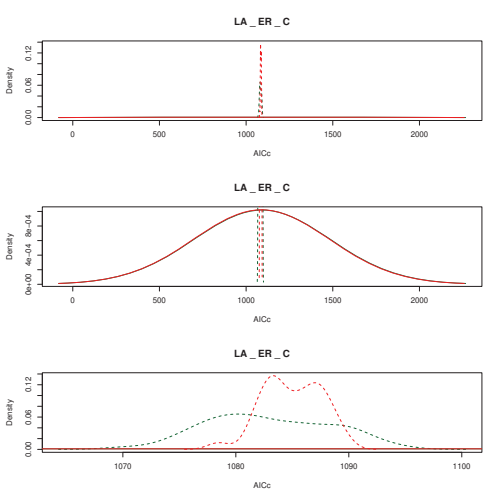
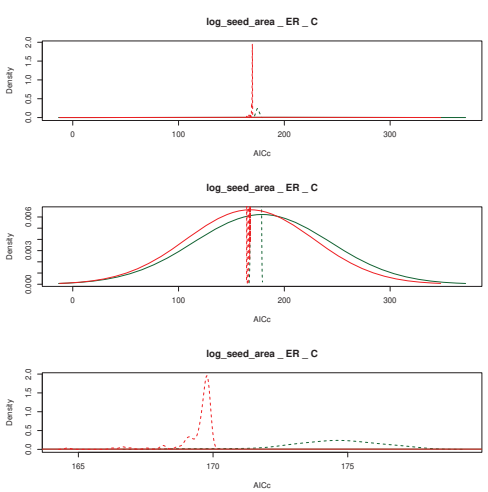

LA _ ER _ C
Density
AICc

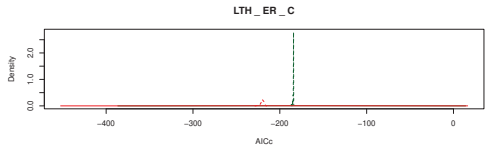
LA _ ER _ C
Density
AICc

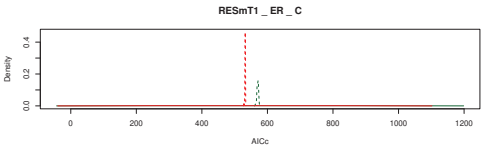
LA _ ER _ C
Density
AICc

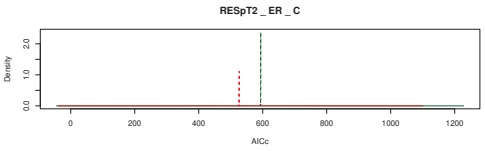

log_seed_area _ ER _ C
Density
AICc

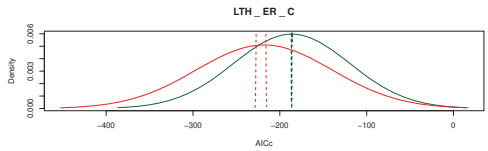
log_seed_area _ ER _ C
Density
AICc

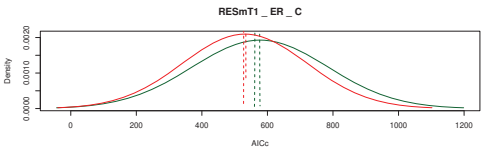
log_seed_area _ ER _ C
Density
AICc


LTH _ ER _ C
Density
AICc


RESmT1 _ ER _ C
Density
AICc


RESpT2 _ ER _ C
Density
AICc


LTH _ ER _ C
Density
AICc


RESmT1 _ ER _ C
Density
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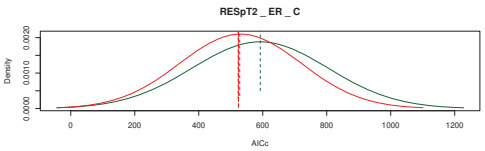
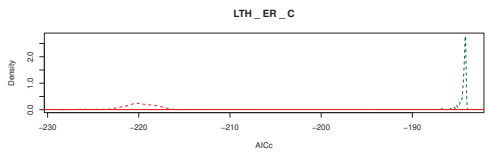

RESpT2 _ ER _ C
Density
AICc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Density
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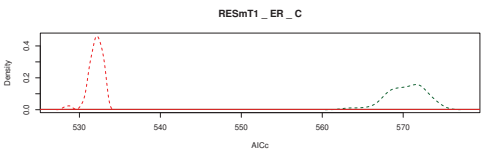
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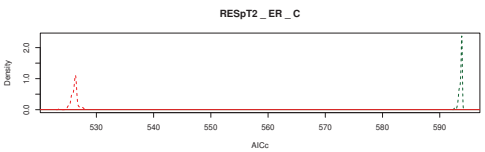
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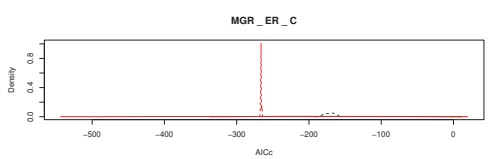
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Density
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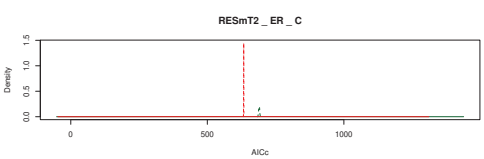
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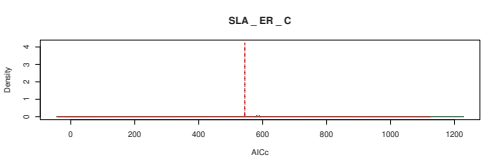
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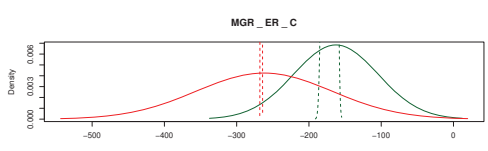
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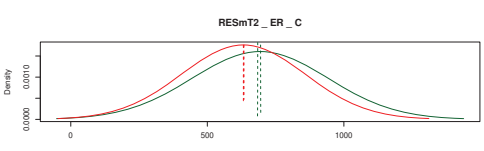
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Density
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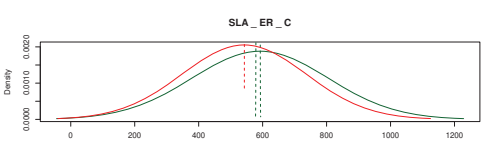
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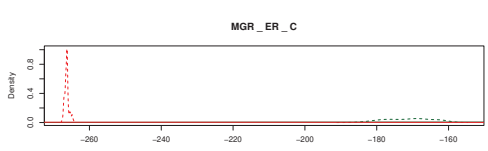
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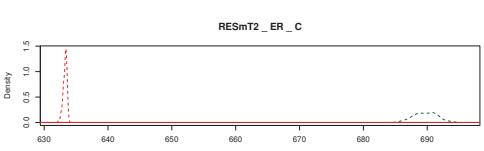
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Density
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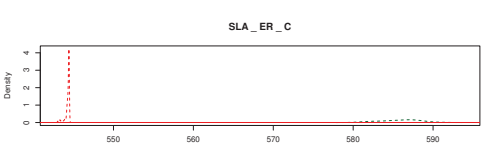
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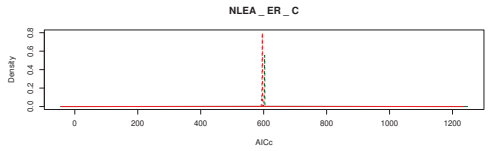
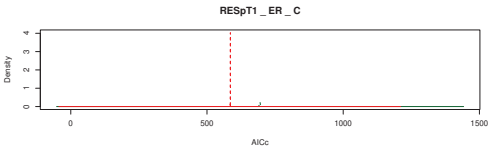

NLEA _ ER _ C
Density
AICc


RESpT1 _ ER _ C
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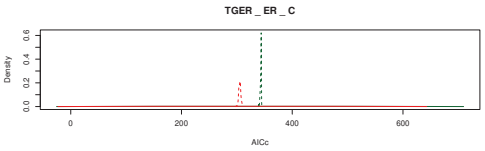
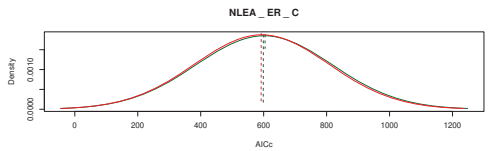

TGER _ ER _ C
Density
AICc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Density
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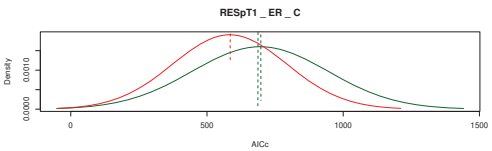
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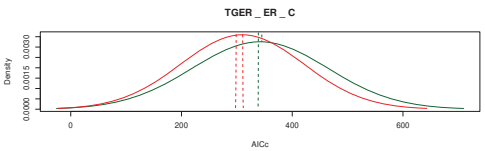
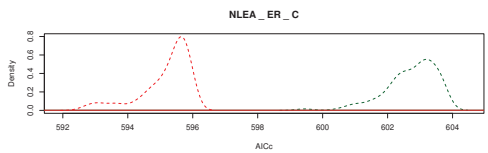

TGER _ ER _ C
Density
AICc


NLEA _ ER _ C
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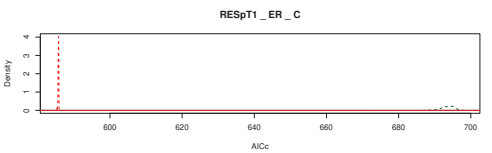
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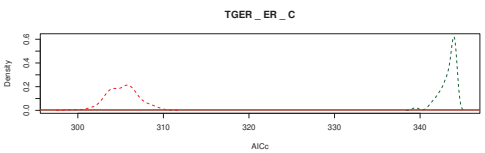
TGER _ ER _ C
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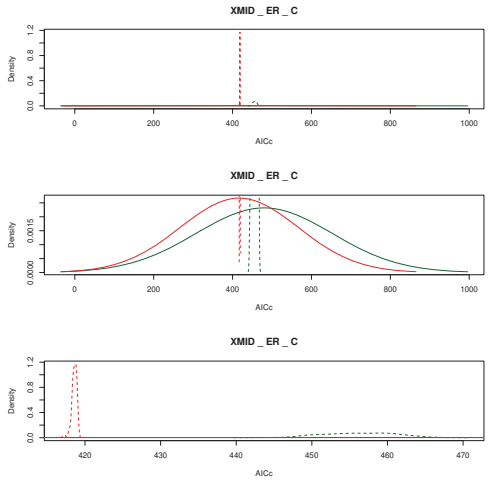
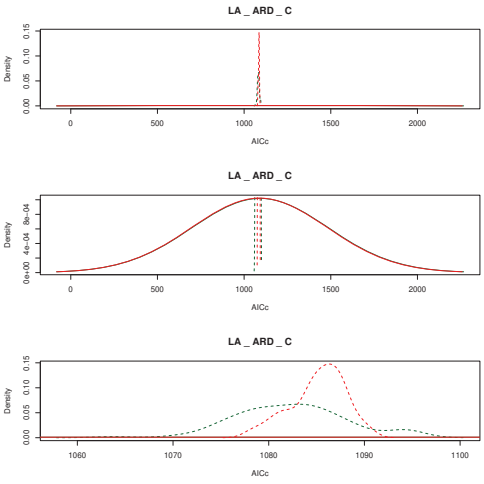
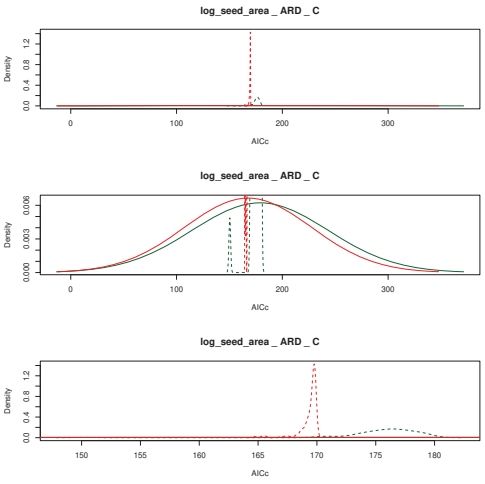

XMID _ ER _ C
Density
AICc


LA _ ARD _ C
Density
AICc


log_seed_area _ ARD _ C
Density
AICc

XMID _ ER _ C
Density
AICc

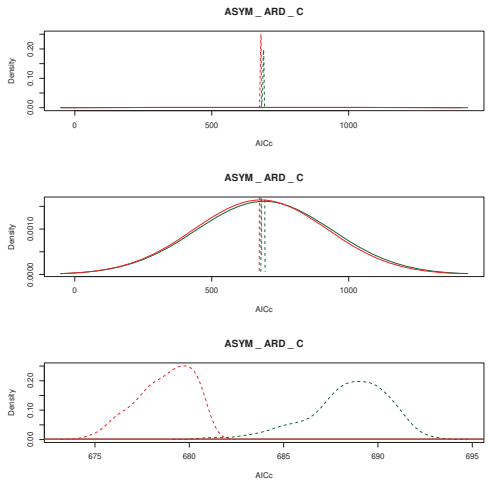
LA _ ARD _ C
Density
AICc

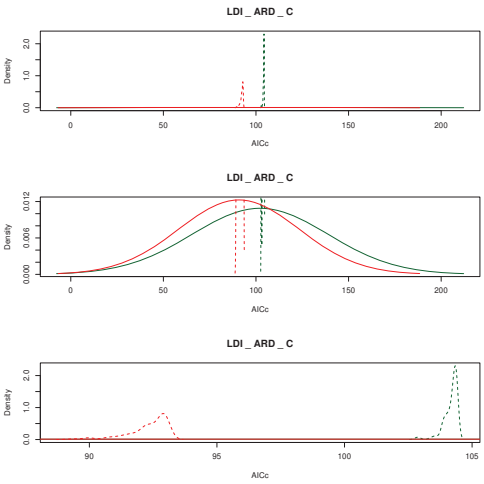
log_seed_area _ ARD _ C
Density
AICc

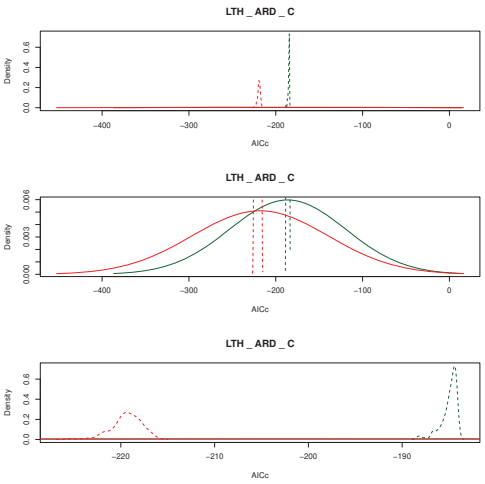
XMID _ ER _ C
Density
AICc

LA _ ARD _ C
Density
AICc

log_seed_area _ ARD _ C
Density
AICc


ASYM _ ARD _ C
Density
AICc


LDI _ ARD _ C
Density
AICc


LTH _ ARD _ C
Density
AICc

ASYM _ ARD _ C
Density
AICc

LDI _ ARD _ C
Density
AICc

LTH _ ARD _ C
Density
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Density
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LTH _ ARD _ C
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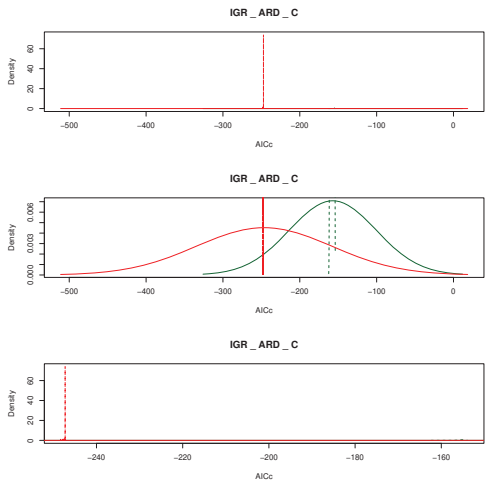
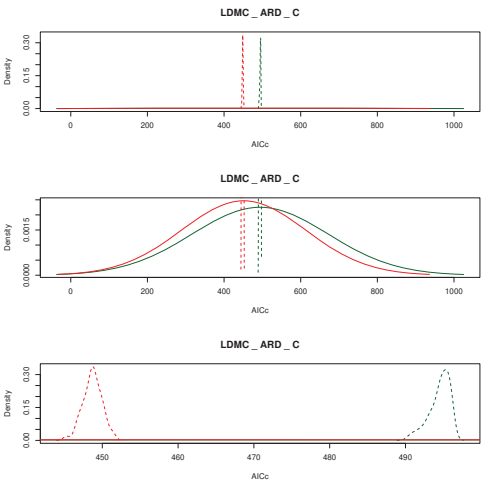
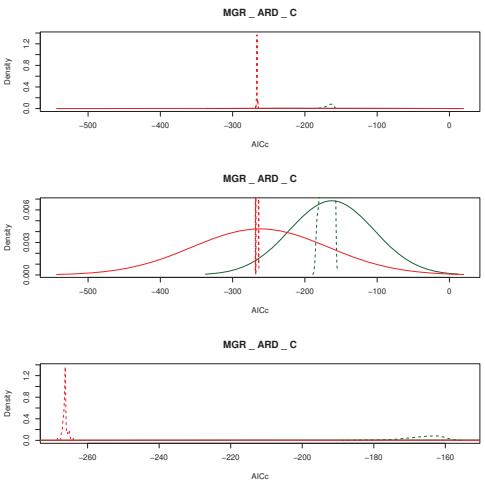

IGR _ ARD _ C
Density
AICc


LDMC _ ARD _ C
Density
AICc


MGR _ ARD _ C
Density
AICc

IGR _ ARD _ C
Density
AICc

LDMC _ ARD _ C
Density
AICc

MGR _ ARD _ C
Density
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IGR _ ARD _ C
Density
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LDMC _ ARD _ C
Density
AICc

MGR _ ARD _ C
Density
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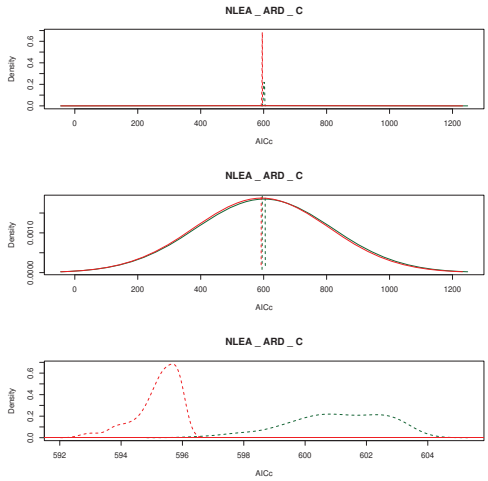
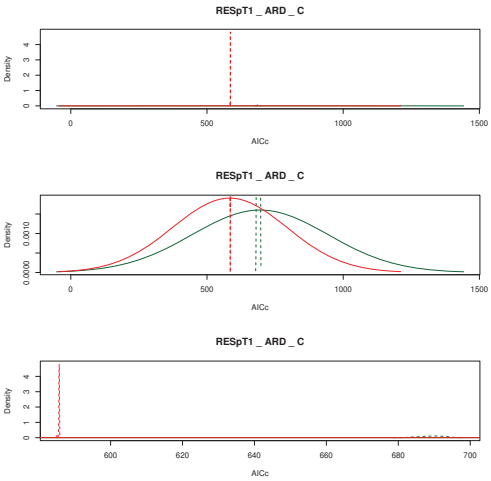
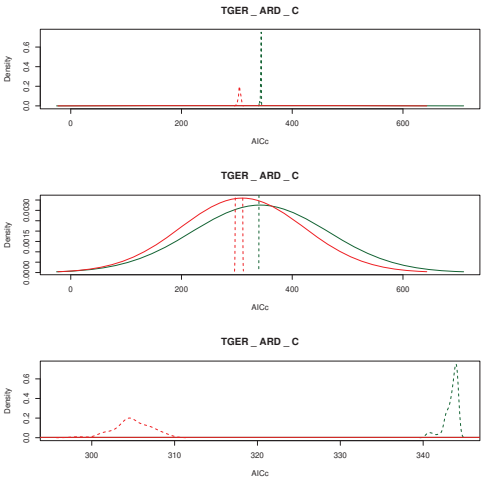

NLEA _ ARD _ C
Density
AICc


RESpT1 _ ARD _ C
Density
AICc


TGER _ ARD _ C
Density
AICc

NLEA _ ARD _ C
Density
AICc

RESpT1 _ ARD _ C
Density
AICc

TGER _ ARD _ C
Density
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RESpT1 _ ARD _ C
Density
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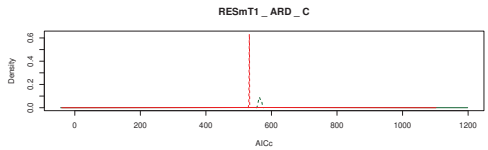
RESmT1 _ ARD _ C
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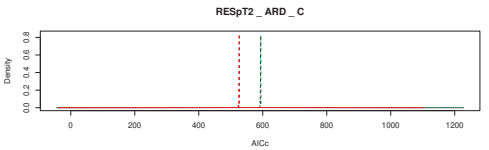
RESpT2 _ ARD _ C
Density
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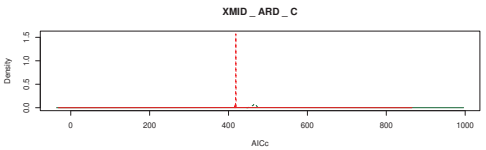
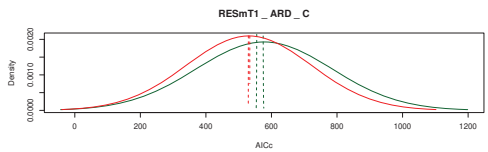

XMID _ ARD _ C
Density
AICc


RESmT1 _ ARD _ C
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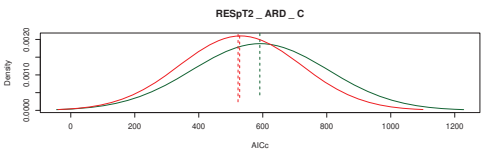
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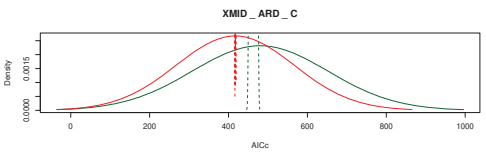
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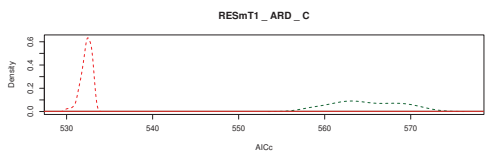
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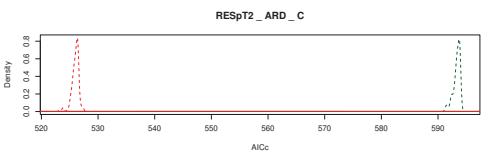
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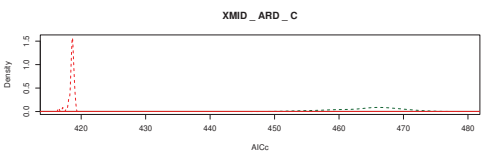
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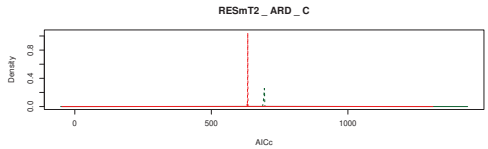
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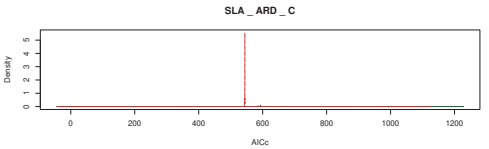
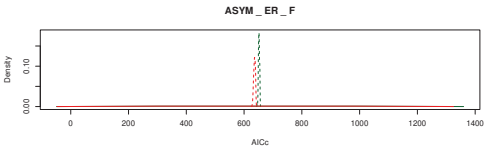
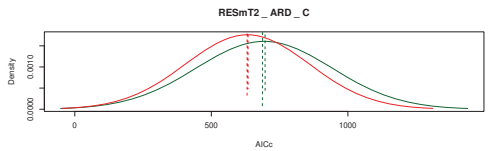

SLA _ ARD _ C
Density
AICc


ASYM _ ER _ F
Density
AICc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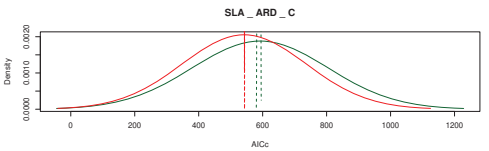
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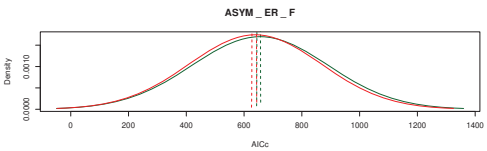
ASYM _ ER _ F
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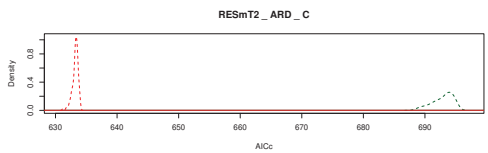
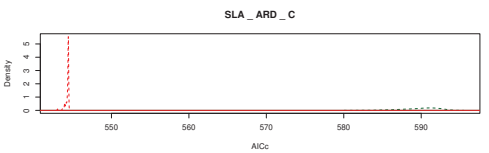

RESmT2 _ ARD _ C
Density
AICc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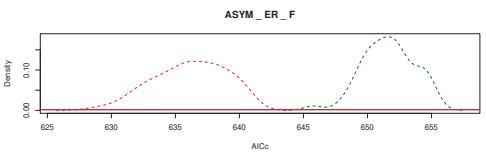
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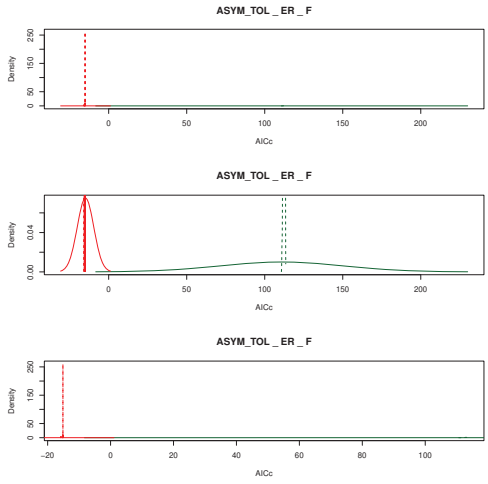
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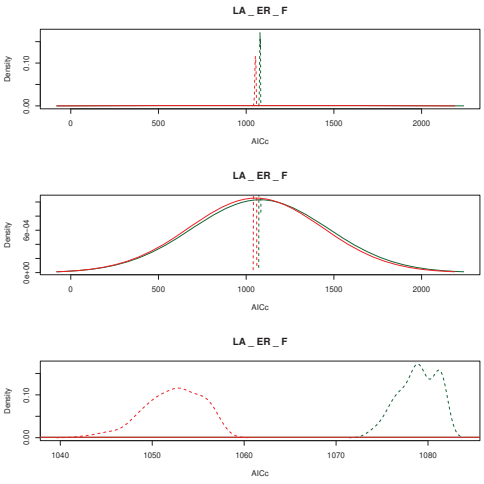
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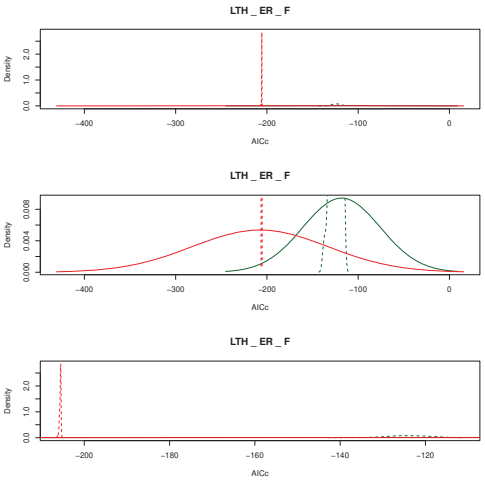
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ASYM_TOL _ ER _ F
Density
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LA _ ER _ F
Density
AICc

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Density
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Density
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Density
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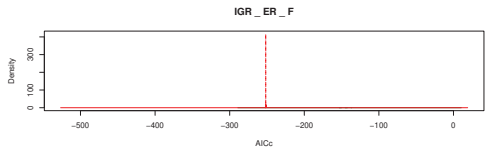
Density
AICc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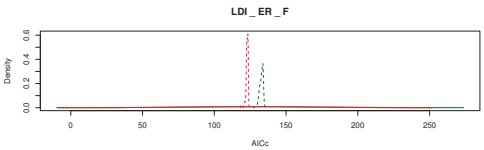
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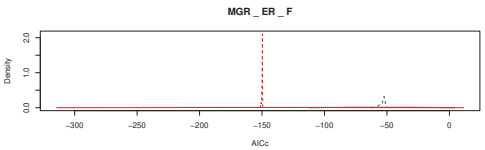
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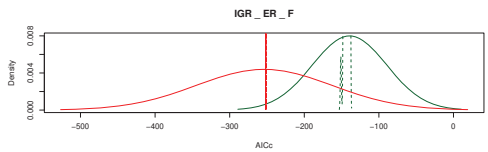
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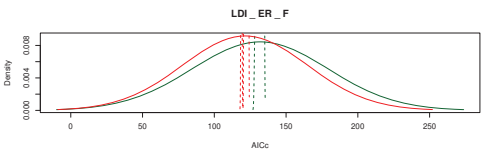
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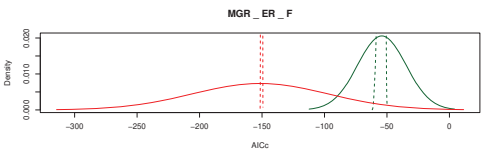
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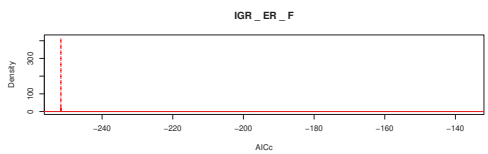
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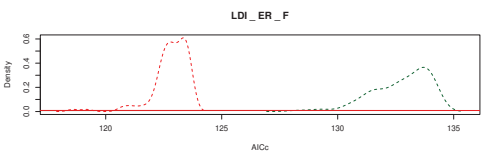
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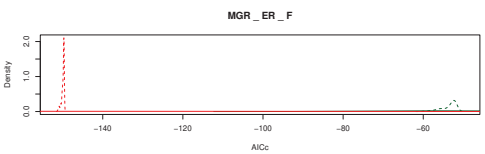
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Density
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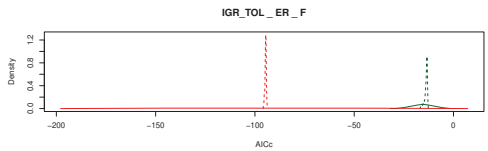
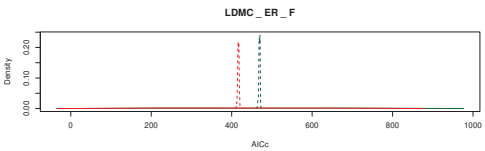

IGR_TOL _ ER _ F
Density
AICc


LDMC _ ER _ F
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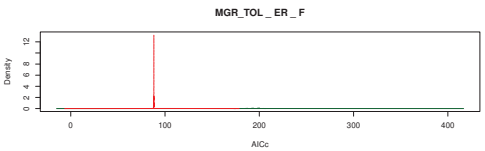
MGR_TOL _ ER _ F
Density
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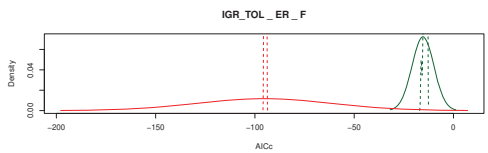
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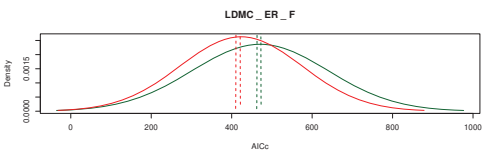
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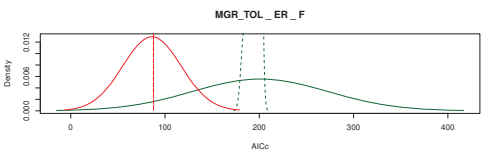
Density
AICc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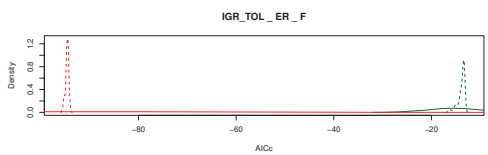
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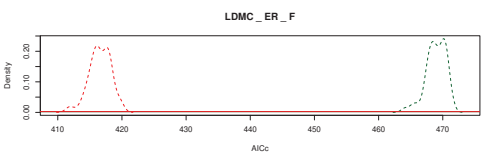
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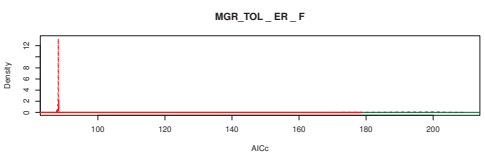
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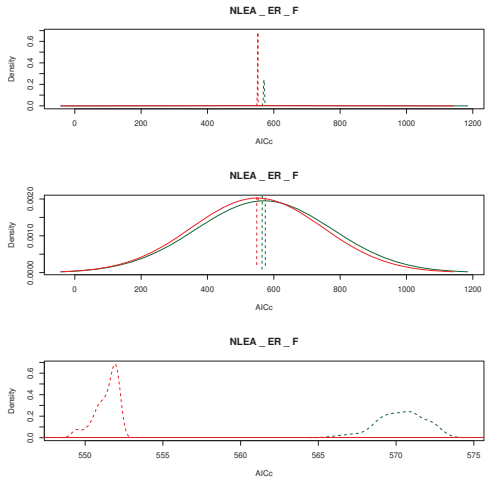
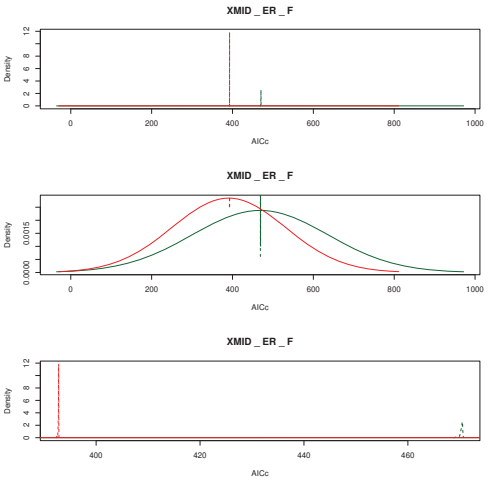
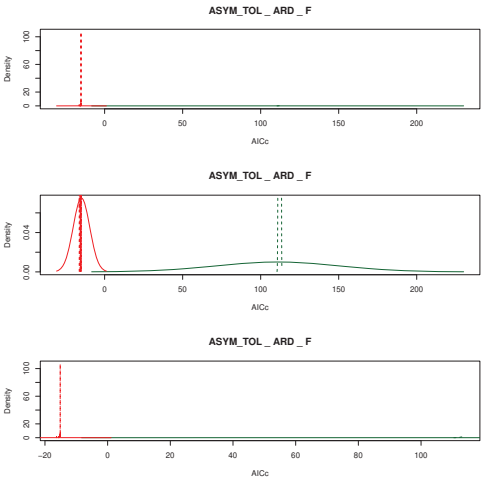

NLEA _ ER _ F
Density
AICc


XMID _ ER _ F
Density
AICc


ASYM_TOL _ ARD _ F
Density
AICc

NLEA _ ER _ F
Density
AICc

XMID _ ER _ F
Density
AICc

ASYM_TOL _ ARD _ F
Density
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Density
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XMID _ ER _ F
Density
AICc

ASYM_TOL _ ARD _ F
Density
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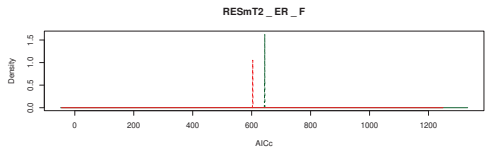
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Density
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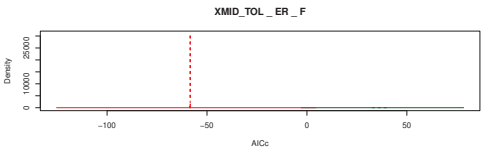
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Density
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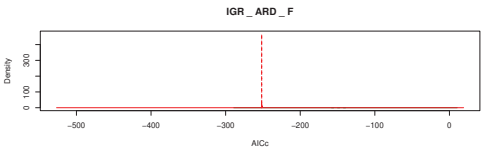
IGR _ ARD _ F
Density
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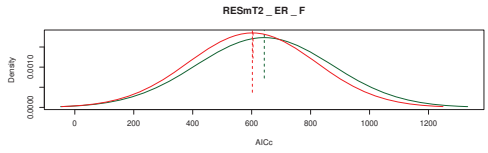
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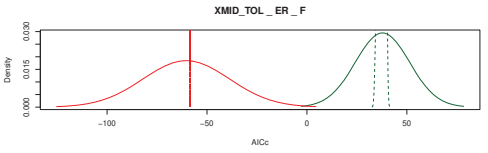
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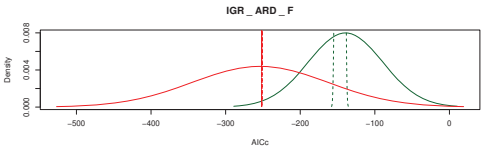
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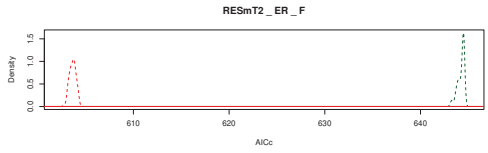
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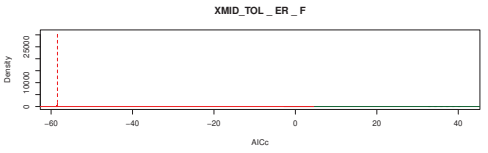
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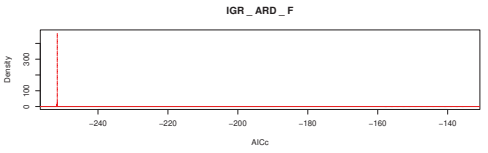
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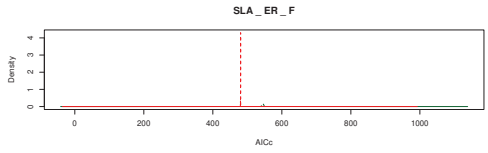
SLA _ ER _ F
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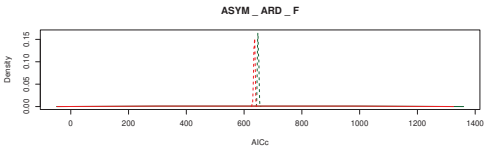
ASYM _ ARD _ F
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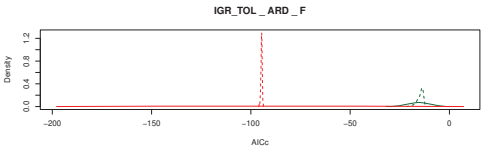
IGR_TOL _ ARD _ F
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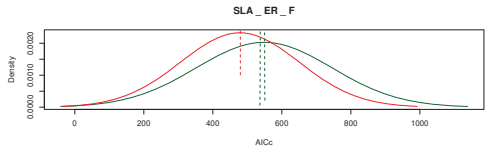
SLA _ ER _ F
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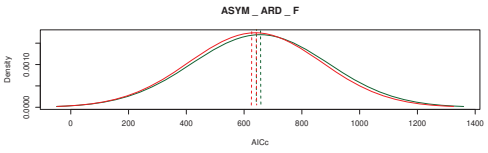
ASYM _ ARD _ F
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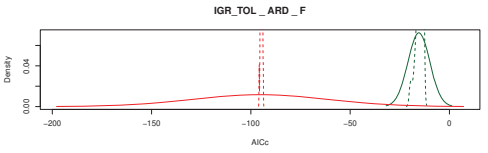
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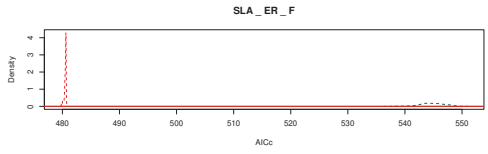
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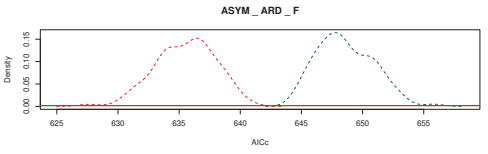
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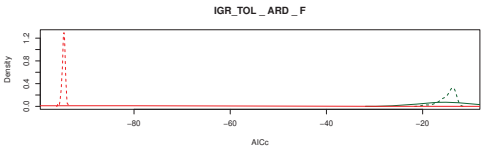
IGR_TOL _ ARD _ F
Density
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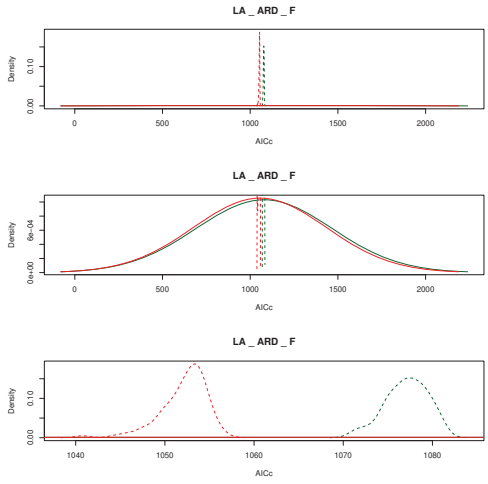
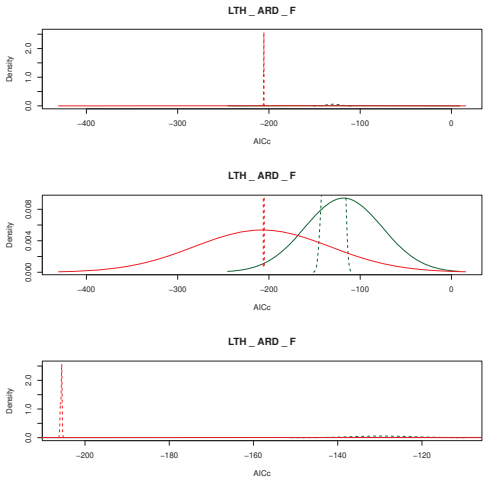

LA _ ARD _ F
Density
AICc

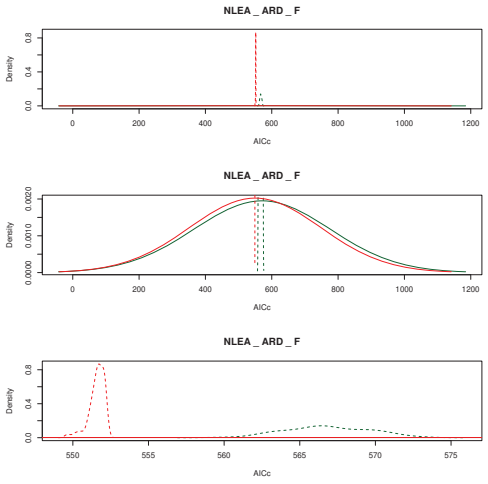
LA _ ARD _ F
Density
AICc

LA _ ARD _ F
Density
AICc


LTH _ ARD _ F
Density
AICc

LTH _ ARD _ F
Density
AICc

LTH _ ARD _ F
Density
AICc


NLEA _ ARD _ F
Density
AICc

NLEA _ ARD _ F
Density
AICc

NLEA _ ARD _ F
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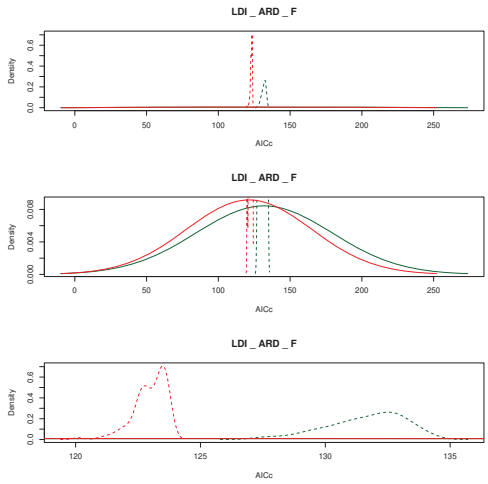
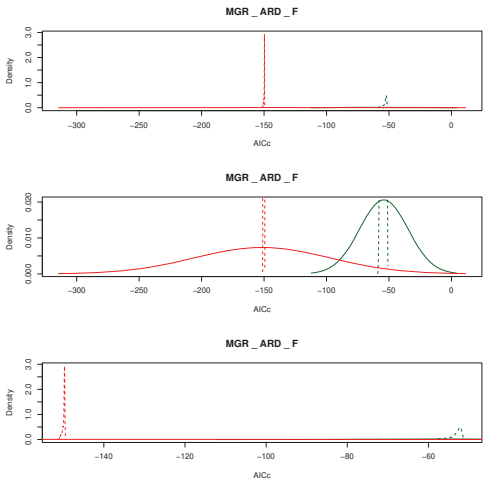

LDI _ ARD _ F
Density
AICc

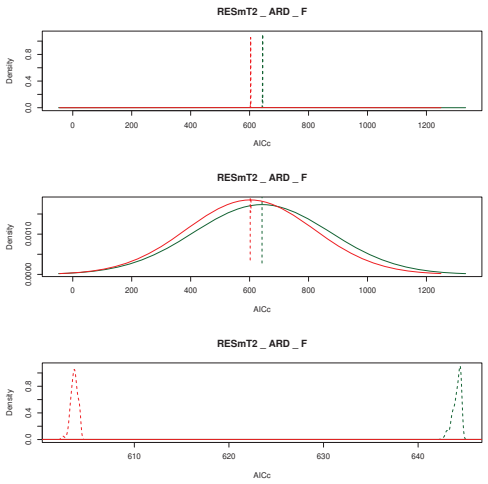
LDI _ ARD _ F
Density
AICc

LDI _ ARD _ F
Density
AICc


MGR _ ARD _ F
Density
AICc

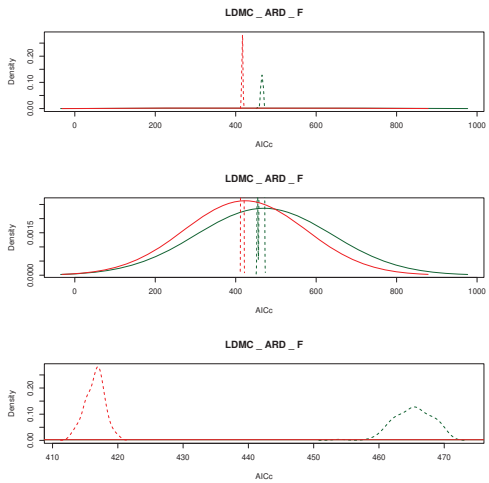
MGR _ ARD _ F
Density
AICc

MGR _ ARD _ F
Density
AICc


RESmT2 _ ARD _ F
Density
AICc

RESmT2 _ ARD _ F
Density
AICc

RESmT2 _ ARD _ F
Density
AICc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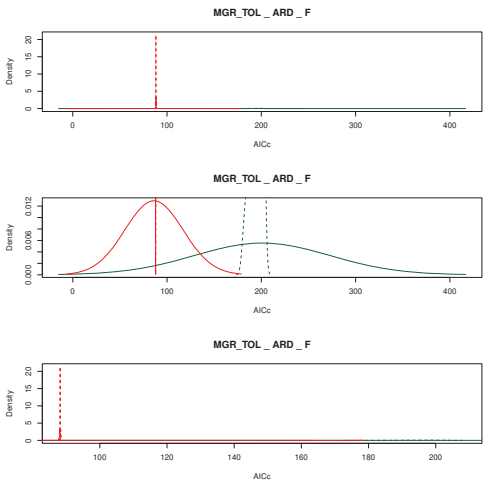
LDMC _ ARD _ F
Density
AICc

LDMC _ ARD _ F
Density
AICc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MGR_TOL _ ARD _ F
Density
AICc

MGR_TOL _ ARD _ F
Density
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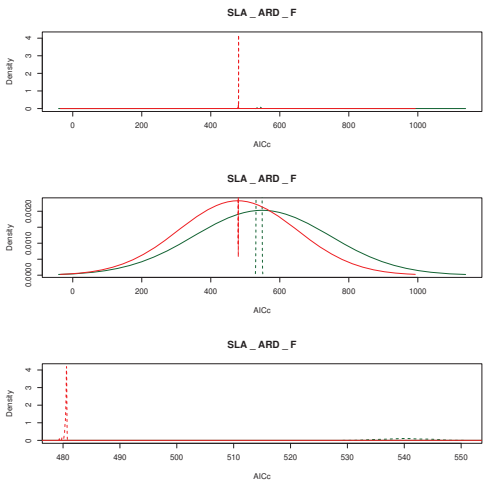
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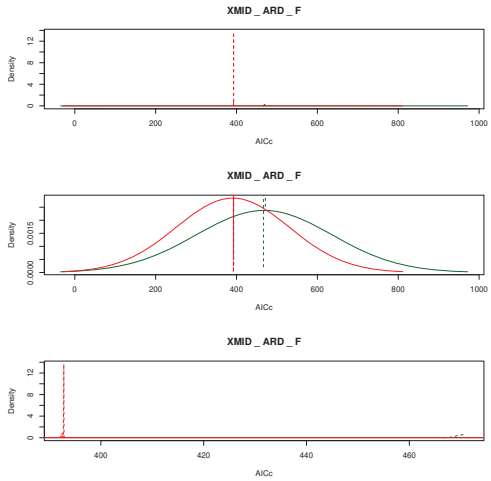
SLA _ ARD _ F
Density
AICc

SLA _ ARD _ F
Density
AICc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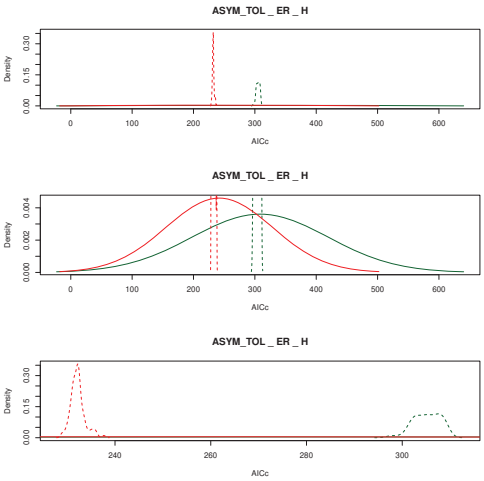
AICc

XMID _ ARD _ F
Density
AICc

XMID _ ARD _ F
Density
AICc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AICc

ASYM_TOL _ ER _ H
Density
AICc

ASYM_TOL _ ER _ H
Density
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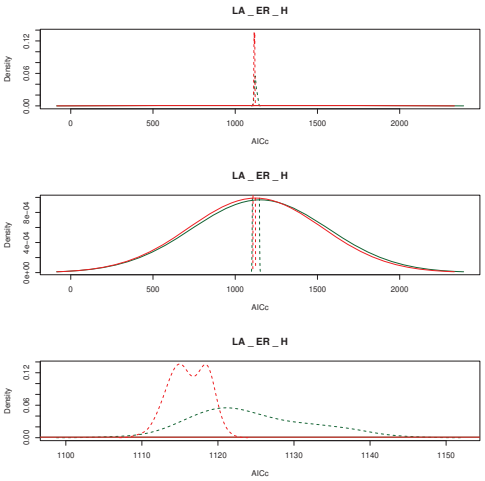
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AICc

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Density
AICc

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Density
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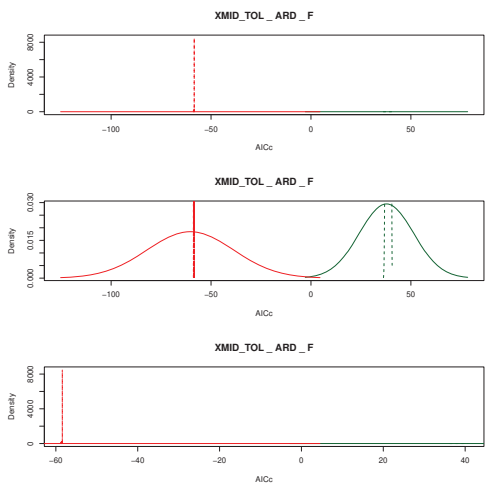
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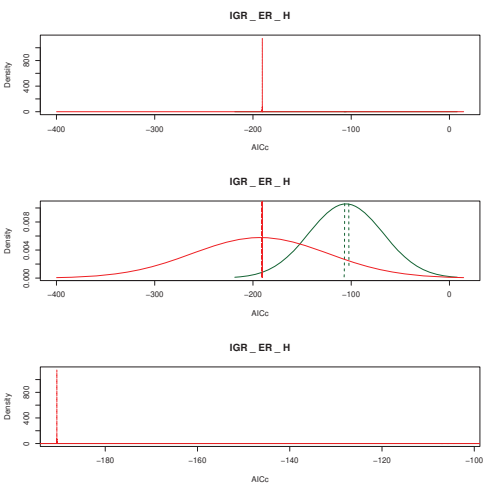
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Density
AICc

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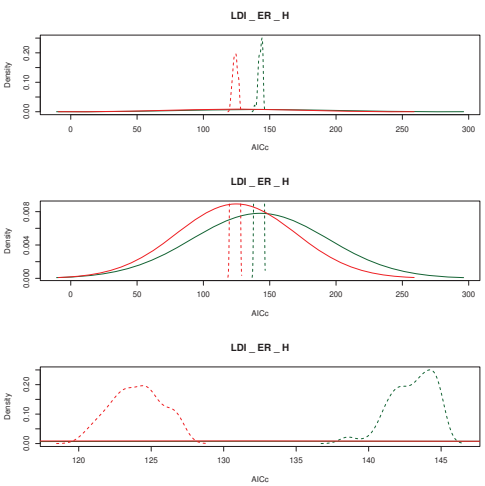
AICc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Density
AICc

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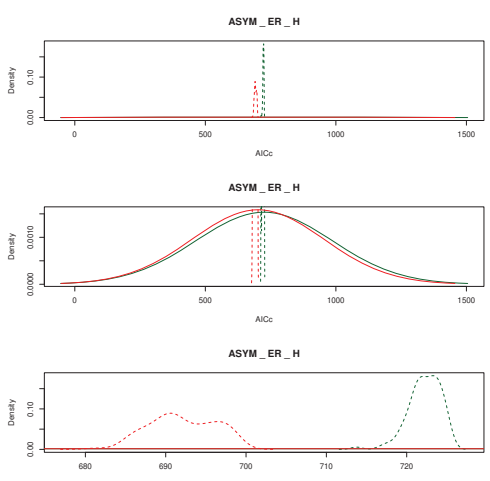
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AICc

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Density
AICc

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Density
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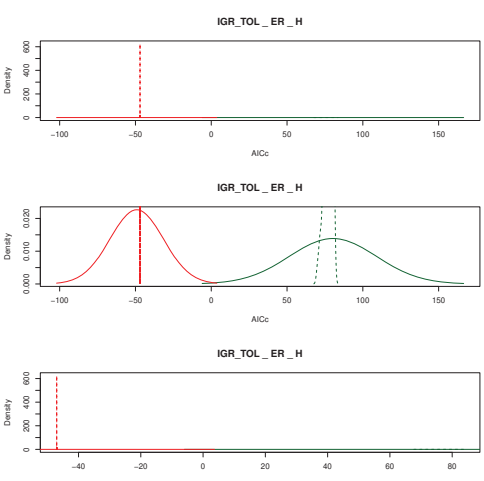
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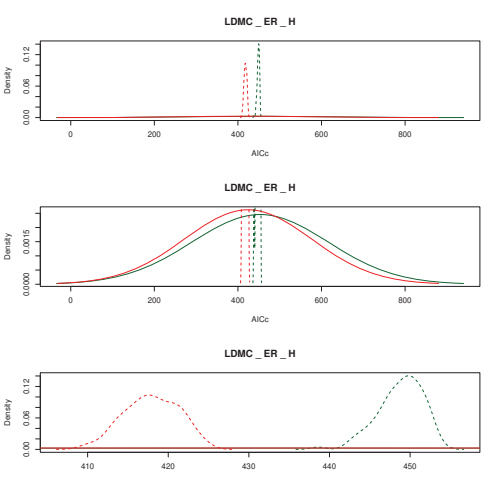
LDMC _ ER _ H
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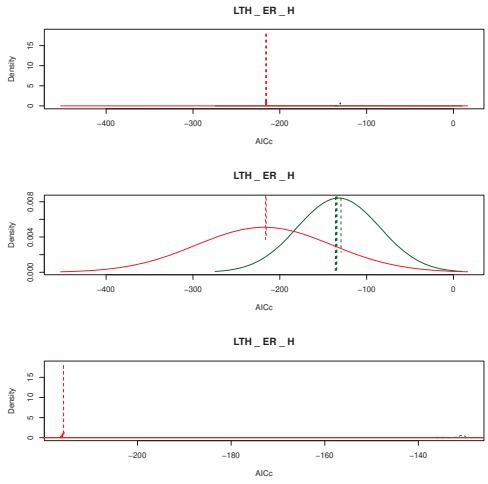
AICc

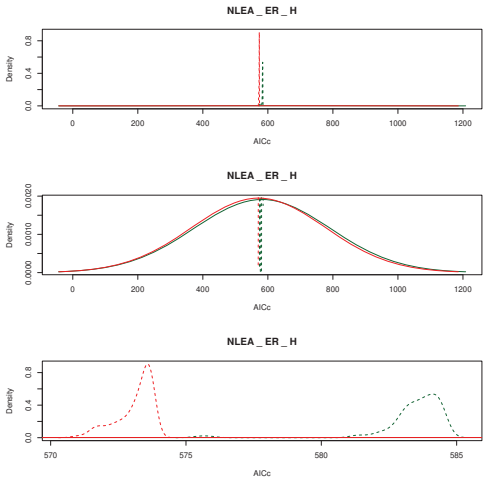
LDMC _ ER _ H
Density
AICc

LDMC _ ER _ H
Density
AICc


LTH _ ER _ H
Density
AICc

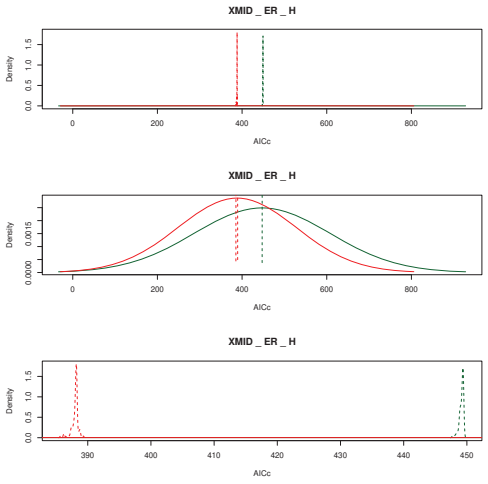
LTH _ ER _ H
Density
AICc

LTH _ ER _ H
Density
AICc


NLEA _ ER _ H
Density
AICc

NLEA _ ER _ H
Density
AICc

NLEA _ ER _ H
Density
AICc


XMID _ ER _ H
Density
AICc

XMID _ ER _ H
Density
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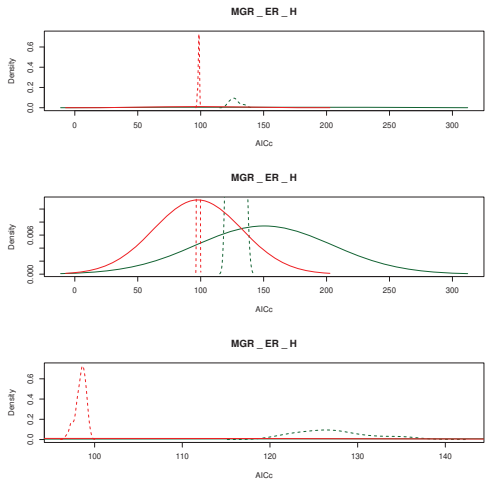
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AICc

MGR _ ER _ H
Density
AICc

MGR _ ER _ H
Density
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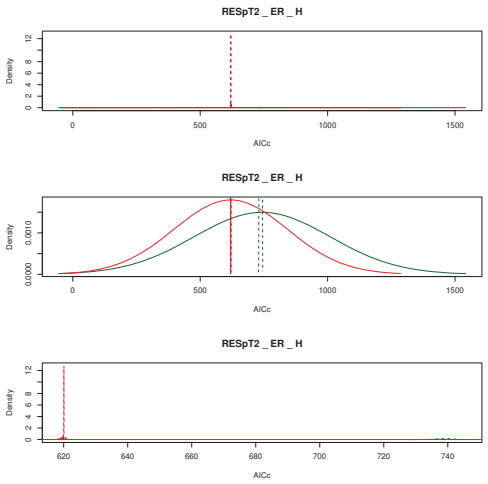
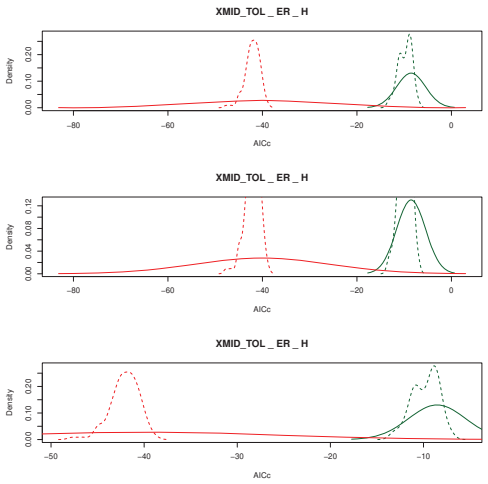

RESpT2 _ ER _ H
Density
AICc

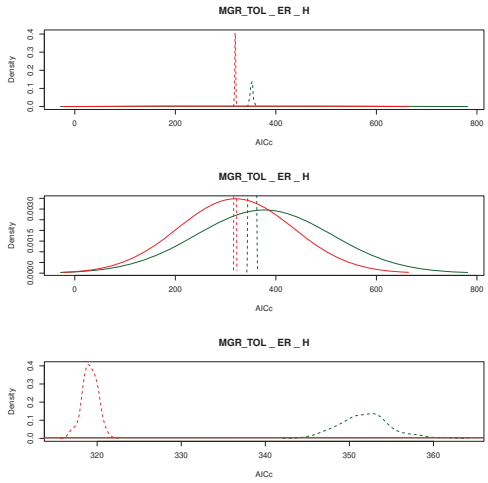
RESpT2 _ ER _ H
Density
AICc

RESpT2 _ ER _ H
Density
AICc


XMID_TOL _ ER _ H
Density
AICc

XMID_TOL _ ER _ H
Density
AICc

XMID_TOL _ ER _ H
Density
AICc


MGR_TOL _ ER _ H
Density
AICc

MGR_TOL _ ER _ H
Density
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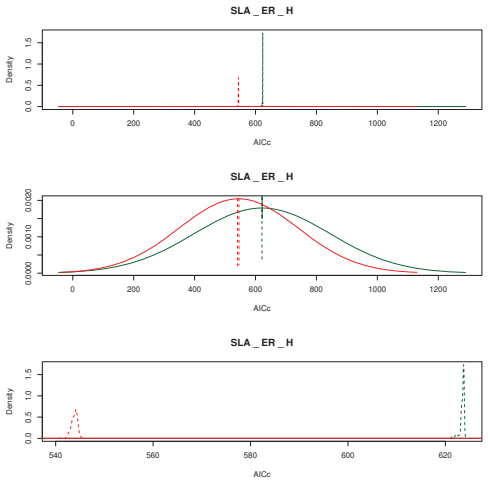
SLA _ ER _ H
Density
AICc

SLA _ ER _ H
Density
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SLA _ ER _ H
Density
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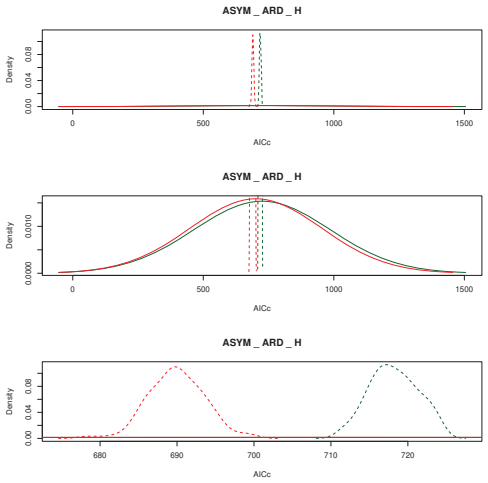
ASYM _ ARD _ H
Density
AICc

ASYM _ ARD _ H
Density
AICc

ASYM _ ARD _ H
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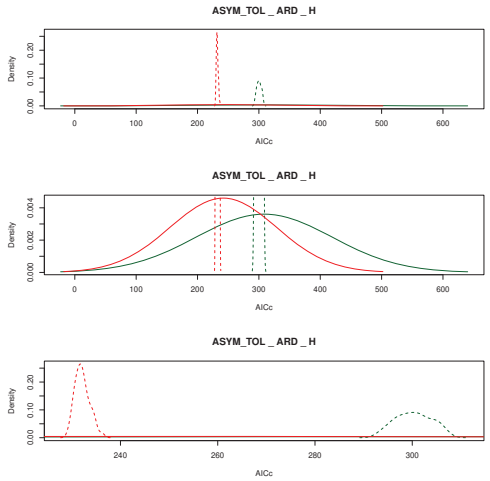
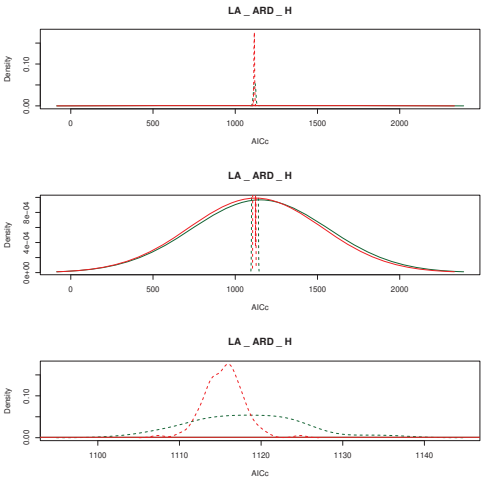
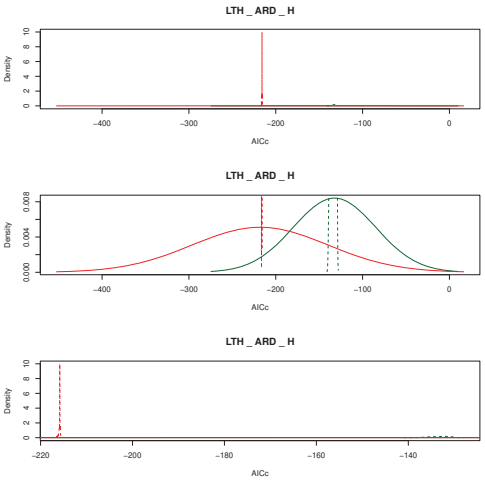

ASYM_TOL _ ARD _ H
Density
AICc

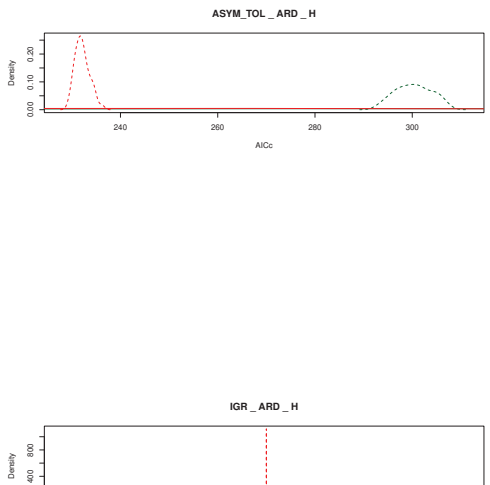

LA _ ARD _ H
Density
AICc


LTH _ ARD _ H
Density
AICc

ASYM_TOL _ ARD _ H
Density
AICc

LA _ ARD _ H
Density
AICc

LTH _ ARD _ H
Density
AICc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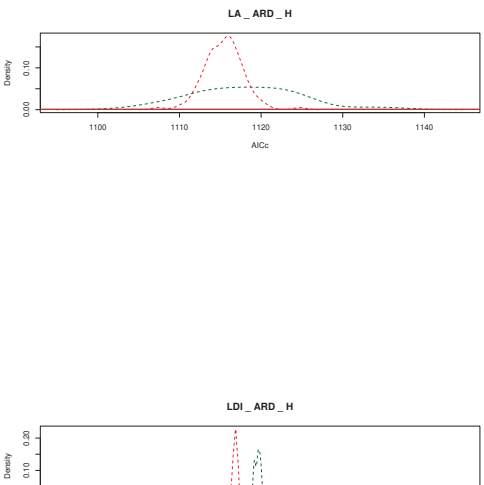
AICc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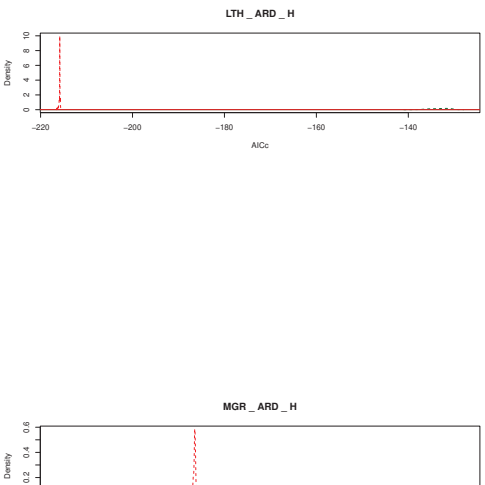
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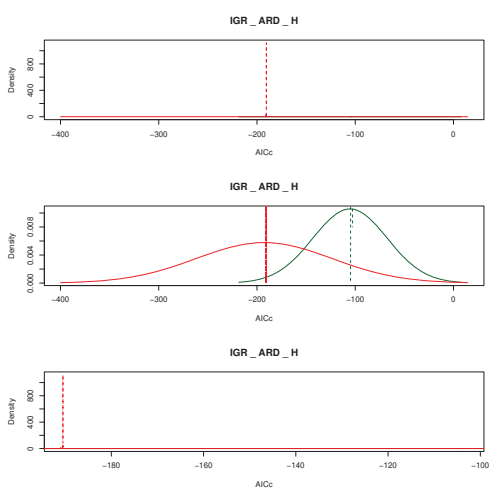
IGR _ ARD _ H
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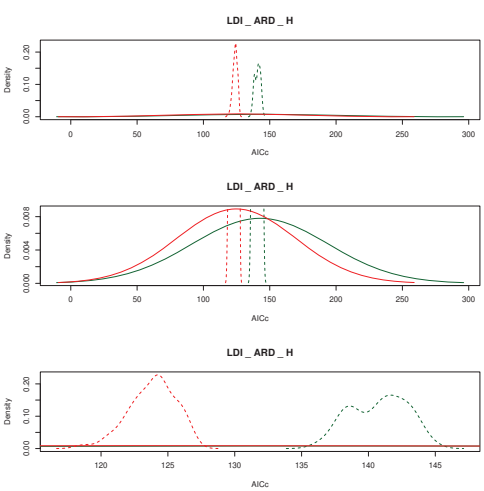
AICc


LDI _ ARD _ H
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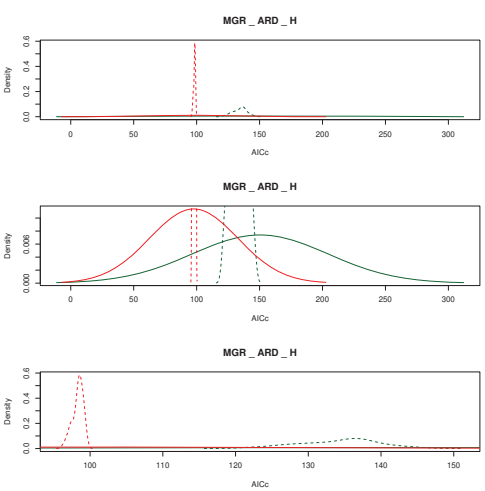
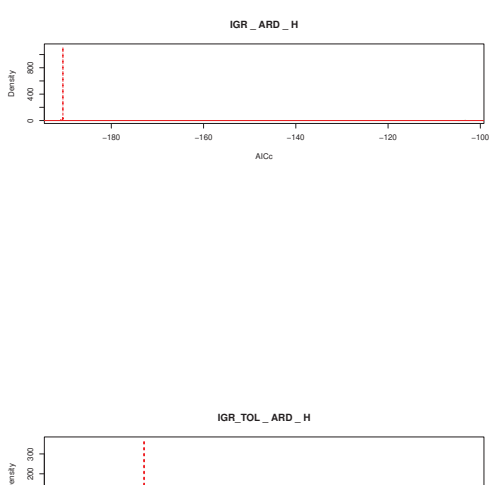
AICc


MGR _ ARD _ H
Density
AICc

IGR _ ARD _ H
Density
AICc

LDI _ ARD _ H
Density
AICc

MGR _ ARD _ H
Density
AICc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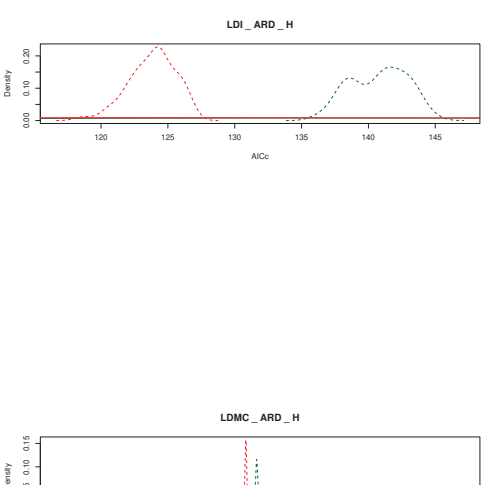
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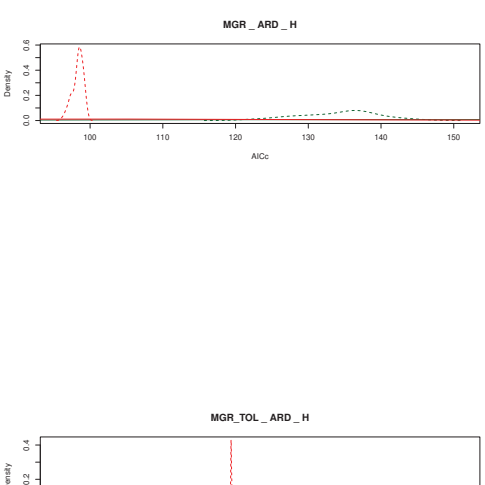
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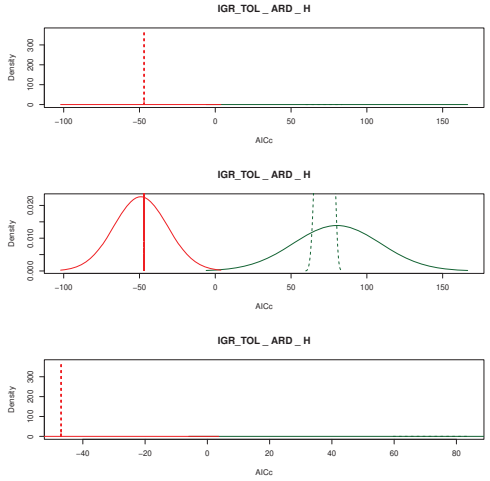
IGR_TOL _ ARD _ H
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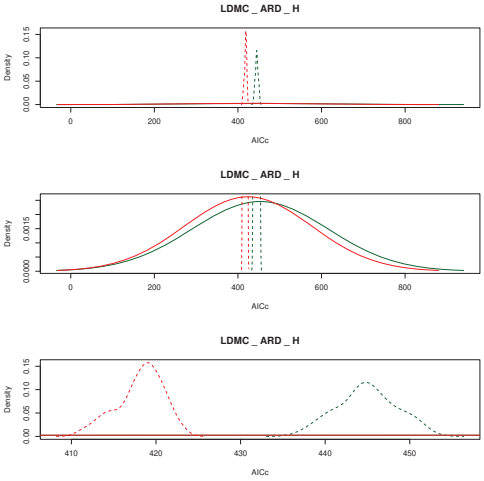
AICc


LDMC _ ARD _ H
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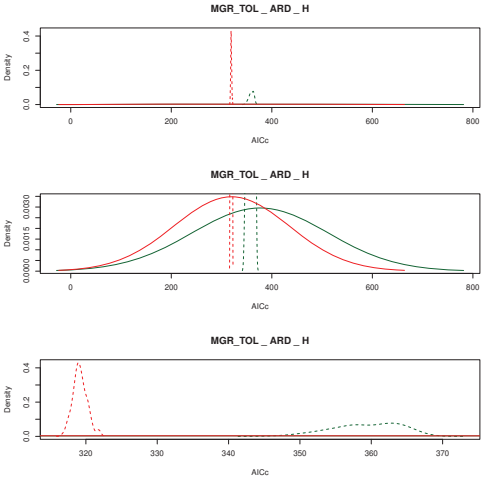
AICc


MGR_TOL _ ARD _ H
Density
AICc

IGR_TOL _ ARD _ H
Density
AICc

LDMC _ ARD _ H
Density
AICc

MGR_TOL _ ARD _ H
Density
AICc

IGR_TOL _ ARD _ H
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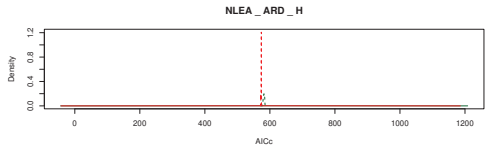
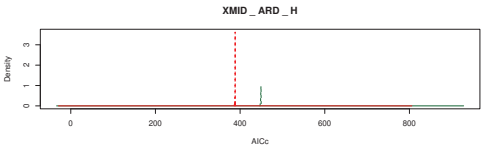
LDMC _ ARD _ H
Density
AICc

MGR_TOL _ ARD _ H
Density
AICc


NLEA _ ARD _ H
Density
AICc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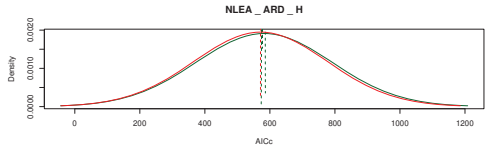
AICc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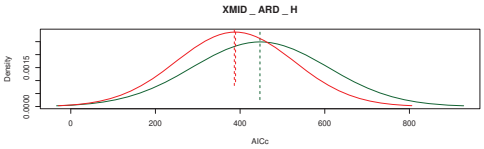
XMID _ ARD _ H
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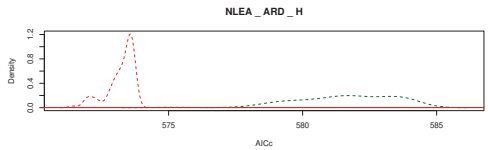
NLEA _ ARD _ H
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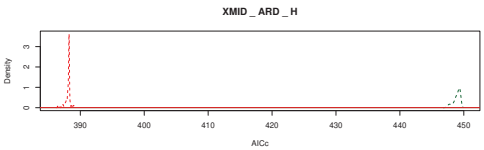
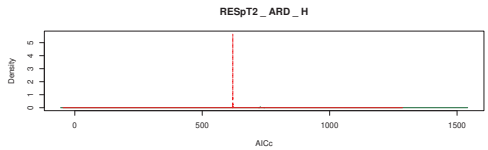
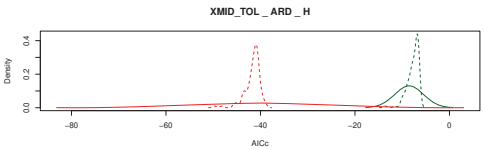
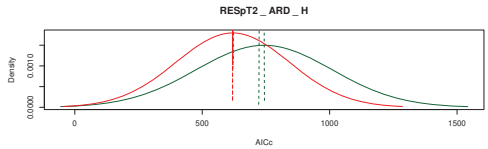
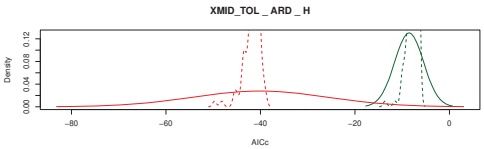

XMID _ ARD _ H
Density
AICc


RESpT2 _ ARD _ H
Density
AICc


XMID_TOL _ ARD _ H
Density
AICc


RESpT2 _ ARD _ H
Density
AICc


XMID_TOL _ ARD _ H
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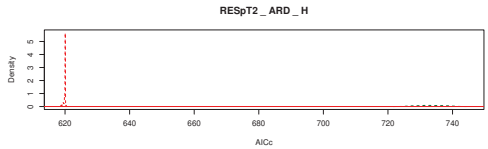
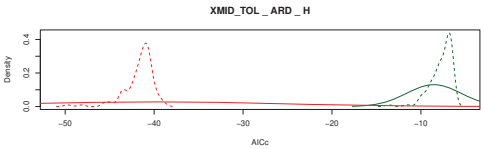
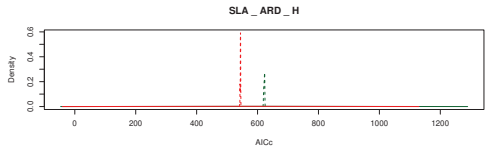
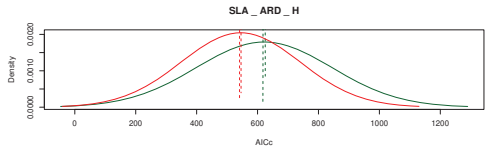
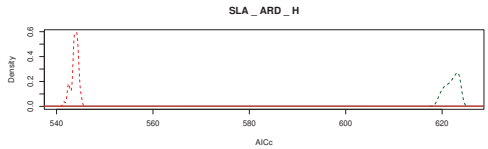

RESpT2 _ ARD _ H
Density
AICc


XMID_TOL _ ARD _ H
Density
AICc


SLA _ ARD _ H
Density
AICc


SLA _ ARD _ H
Density
AICc


SLA _ ARD _ H
Density
AICc

Effect of temperature on half-life - A5 (Chapter 1)

Effect of temperature during growth (regular Frost [F], mild [M] and regular heat [H]) on phylogenetic half-life. Phylogenetic half-life was revealed for sowing S2, from OU1 + OUM models of each trait on 100 independent stochastic character maps with "high" and "low" as evolutionary regimes. Half-life was cube-root transformed. Posterior mean reflects the effect of frost or heat compared to mild conditions.

Fixed effects	**Mean (±SD)**	**Signif.**	**Lower-95 CI**	**Upper-95 CI**
intercept	1.17 (± 0.23)	***	0.71	1.63
frost (F; -2°C 1h)	-0.44 (± 0.19)	*	-0.85	-0.11
heat (H; +40°C 1h)	-0.17 (± 0.17)		-0.51	0.17
Random effects				
traits	0.37 (± 0.24)		0.09	0.84
traits:mild(M; +20°C)	0.17 (± 0.14)		0.00	0.44
traits:frost(F; -2°C 1h)	0.13 (± 0.12)		0.00	0.35
traits:heat(H; +40°C 1h)	0.08 (± 0.11)		0.00	0.29
residuals	0.01 (± 0.0)		0.01	0.01

Significance (pMCMC): * < 0.05, ** < 0.01, *** < 0.001

Evolutionary half-life of traits (± standard deviation)

		Treatment								
		Frost			**Mild**			**Heat**		
	Trait ID	S1	S2	Global	S1	S2	Global	S1	S2	Global
	SSIZ	. .	. .	. .	10.818 ± 0.242 *	6.007 ± 0.150 *	8.412 ± 0.065 *	. .	. .	. .
	TGER	. .	. .	. .	0.006 ± 0.003 *	2.157 ± 0.434 *	1.081 ± 0.305 *	. .	. .	. .
Growth	IGR	. .	0.024 ± 0.011 *	. .	. .	0.090 ± 0.065 ns	. .	. .	0.030 ± 0.008 *	. .
Growth	MGR	4.645 ± 0.232 *	0.066 ± 0.052 ns	2.355 ± 0.127 *	0.006 ± 0.005 ns	0.173 ± 0.066 *	0.090 ± 0.043 *	0.471 ± 0.062 *	0.995 ± 0.038 *	0.733 ± 0.017 *
Growth	XMID	0.254 ± 0.159 ns	0.062 ± 0.029 *	0.158 ± 0.092 *	0.002 ± 0.000 *	0.690 ± 0.031 *	0.346 ± 0.022 *	0.064 ± 0.045 ns	0.329 ± 0.190 *	0.196 ± 0.103 *
Growth	ASYM	1.655 ± 0.644 *	5.182 ± 0.893 *	3.419 ± 0.176 *	5.578 ± 1.211 *	6.447 ± 0.602 *	6.013 ± 0.431 *	17.108 ± 5.246 *	4.152 ± 1.498 *	10.630 ± 2.650 *
Growth	NLEA	. .	3.709 ± 0.054 *	. .	. .	7.148 ± 0.108 *	. .	. .	5.992 ± 0.063 *	. .
Leaf traits	LA	1.154 ± 0.374 *	3.303 ± 0.558 *	2.228 ± 0.130 *	3.682 ± 1.080 *	9.950 ± 1.902 *	6.816 ± 0.581 *	19.636 ± 4.189 *	2.891 ± 1.305 *	11.264 ± 2.039 *
Leaf traits	SLA	4.802 ± 0.182 *	0.693 ± 0.011 *	2.747 ± 0.121 *	1.924 ± 0.050 *	1.527 ± 0.031 *	1.725 ± 0.013 *	0.275 ± 0.012 *	0.531 ± 0.051 *	0.403 ± 0.028 *
Leaf traits	LDMC	2.707 ± 1.342 *	0.756 ± 0.188 *	1.732 ± 0.816 *	0.118 ± 0.046 *	1.475 ± 0.212 *	0.796 ± 0.117 *	0.245 ± 0.211 ns	2.131 ± 0.613 *	1.188 ± 0.284 *
Leaf traits	LTh	. .	0.101 ± 0.032 *	. .	. .	2.502 ± 0.160 *	. .	. .	0.105 ± 0.139 ns	. .
Leaf traits	LDI	2.271 ± 0.220 *	8.029 ± 0.347 *	5.150 ± 0.090 *	0.233 ± 0.048 *	8.460 ± 0.436 *	4.347 ± 0.274 *	8.569 ± 1.766 *	5.629 ± 0.674 *	7.099 ± 0.772 *
Thermal tolerance *s.l.*	RES(-)T1	1.924 ± 0.077 *	. .	. .	. .	1.600 ± 0.079 *	. .	. .	. .	. .
Thermal tolerance *s.l.*	RES(-)T2	1.229 ± 0.610 *	0.952 ± 0.056 *	1.091 ± 0.392 *	. .	0.487 ± 0.102 *	. .	. .	. .	. .
Thermal tolerance *s.l.*	RES(+)T1	. .	. .	. .	. .	0.213 ± 0.243 *	. .	5.008 ± 1.186 *	. .	. .
Thermal tolerance *s.l.*	RES(+)T2	. .	. .	. .	. .	0.202 ± 0.243 ns	. .	0.381 ± 0.216 *	0.068 ± 0.036 *	0.224 ± 0.127 *
Thermal tolerance *s.l.*	TOL_IGR	. .	0.252 ± 0.049 *	. .	. .	. .	. .	. .	0.028 ± 0.011 *	. .
Thermal tolerance *s.l.*	TOL_MGR	3.283 ± 0.109 *	0.090 ± 0.037 *	1.686 ± 0.051 *	. .	. .	. .	0.180 ± 0.099 *	0.858 ± 0.056 *	0.519 ± 0.030 *
Thermal tolerance *s.l.*	TOL_XMID	0.748 ± 0.048 *	0.023 ± 0.011 *	0.386 ± 0.026 *	. .	. .	. .	0.035 ± 0.029 ns	1.875 ± 0.212 *	0.955 ± 0.129 *
Thermal tolerance *s.l.*	TOL_ASYM	0.021 ± 0.006 *	0.020 ± 0.013 ns	0.020 ± 0.005 *	. .	. .	. .	8.119 ± 0.617 *	0.932 ± 0.139 *	4.526 ± 0.338 *

Mean values ± standard deviation (SD) of phylogenetic half-life (estimated from OU1 + OUM) for traits within treatments and rounds of sowing (S1, S2, 'Global'), in units of Mya. A single dot in a cell means that no data was available because the trait was not measured or the best model was of the "BM"-type. Values of phylogenetic half-life are based on models of ARD + ER (for each model, 100 independent stochastic character maps with 'high' and 'low' regime). Detailed information is given in Supplementary material A3. Significance in half-life (*) is given if mean-1.64SD > 0.

Supplementary material – A6 (Chapter 1)

Multi-traits correlations. Traits (from sowing S2) has been first corrected by phylogeny using the function 'pgls' {caper} and for elevation by 'glm'. Residuals were then processed with 'rcorr' {Hmisc} and Pearson's correlation coefficients and the associated *p-value* estimated.
'C' : Mild (20°C); 'F' : Frost (-2°C, 1h); 'H' : Heat (+40°C, 1h). * Indicate sgnificant correlation (*p-value* < 0.05).

trait_1	trait_2	corr. coeff	*p-value*	
ASYM.C	ASYM.F	0.47	0.000	*
ASYM.C	ASYM.H	0.79	0.000	*
ASYM.C	TOL_ASYM.F	-0.38	0.001	*
ASYM.C	TOL_ASYM.H	0.34	0.005	*
ASYM.C	IGR.C	0.18	0.130	
ASYM.C	IGR.F	0.27	0.028	*
ASYM.C	IGR.H	0.01	0.908	
ASYM.C	TOL_IGR.F	0.09	0.441	
ASYM.C	TOL_IGR.H	0.06	0.598	
ASYM.C	LA.C	0.53	0.000	*
ASYM.C	LA.F	0.13	0.292	
ASYM.C	LA.H	0.66	0.000	*
ASYM.C	LDI.C	0.31	0.011	*
ASYM.C	LDI.F	0.08	0.539	
ASYM.C	LDI.H	0.41	0.000	*
ASYM.C	LDMC.C	0.33	0.005	*
ASYM.C	LDMC.F	0.27	0.027	*
ASYM.C	LDMC.H	0.24	0.046	*
ASYM.C	SSIZ.C	-0.04	0.741	
ASYM.C	LTH.C	-0.22	0.064	
ASYM.C	LTH.F	-0.28	0.018	*
ASYM.C	LTH.H	0.11	0.382	
ASYM.C	MGR.C	0.30	0.012	*
ASYM.C	MGR.F	0.06	0.649	
ASYM.C	MGR.H	0.08	0.489	
ASYM.C	TOL_MGR.F	-0.02	0.854	
ASYM.C	TOL_MGR.H	-0.02	0.864	
ASYM.C	NLEA.C	-0.10	0.436	
ASYM.C	NLEA.F	-0.11	0.362	
ASYM.C	NLEA.H	-0.06	0.616	
ASYM.C	RESmT1.C	-0.26	0.033	*
ASYM.C	RESmT2.C	0.26	0.034	*
ASYM.C	RESmT2.F	0.04	0.751	
ASYM.C	RESpT1.C	0.10	0.417	
ASYM.C	RESpT2.C	0.36	0.002	*
ASYM.C	RESpT2.H	0.56	0.000	*
ASYM.C	SLA.C	-0.11	0.390	
ASYM.C	SLA.F	-0.01	0.942	
ASYM.C	SLA.H	-0.12	0.315	
ASYM.C	TGER.C	-0.01	0.946	
ASYM.C	(-)XMID.C	0.19	0.113	
ASYM.C	(-)XMID.F	-0.01	0.915	
ASYM.C	(-)XMID.H	0.19	0.125	
ASYM.C	(-)TOL_XMID.F	-0.13	0.299	
ASYM.C	(-)TOL_XMID.H	0.24	0.051	
ASYM.F	ASYM.H	0.49	0.000	*
ASYM.F	TOL_ASYM.F	0.52	0.000	*
ASYM.F	TOL_ASYM.H	0.09	0.484	
ASYM.F	IGR.C	0.26	0.030	*
ASYM.F	IGR.F	-0.30	0.011	*
ASYM.F	IGR.H	-0.17	0.161	
ASYM.F	TOL_IGR.F	-0.41	0.000	*
ASYM.F	TOL_IGR.H	-0.01	0.964	
ASYM.F	LA.C	0.40	0.001	*
ASYM.F	LA.F	0.04	0.743	
ASYM.F	LA.H	0.05	0.664	
ASYM.F	LDI.C	0.54	0.000	*
ASYM.F	LDI.F	0.30	0.012	*
ASYM.F	LDI.H	0.45	0.000	*
ASYM.F	LDMC.C	0.24	0.050	
ASYM.F	LDMC.F	-0.25	0.040	*
ASYM.F	LDMC.H	0.37	0.002	*
ASYM.F	SSIZ.C	0.16	0.190	
ASYM.F	LTH.C	0.18	0.145	
ASYM.F	LTH.F	0.13	0.277	
ASYM.F	LTH.H	0.05	0.660	
ASYM.F	MGR.C	0.31	0.010	*
ASYM.F	MGR.F	-0.09	0.445	
ASYM.F	MGR.H	0.00	0.995	
ASYM.F	TOL_MGR.F	-0.21	0.087	
ASYM.F	TOL_MGR.H	0.22	0.068	
ASYM.F	NLEA.C	-0.03	0.788	
ASYM.F	NLEA.F	0.02	0.854	
ASYM.F	NLEA.H	-0.08	0.488	
ASYM.F	RESmT1.C	-0.21	0.084	
ASYM.F	RESmT2.C	0.04	0.751	
ASYM.F	RESmT2.F	0.22	0.073	
ASYM.F	RESpT1.C	-0.04	0.738	
ASYM.F	RESpT2.C	0.07	0.574	
ASYM.F	RESpT2.H	0.00	0.997	
ASYM.F	SLA.C	-0.27	0.025	*
ASYM.F	SLA.F	0.08	0.505	
ASYM.F	SLA.H	-0.36	0.002	*
ASYM.F	TGER.C	-0.24	0.050	
ASYM.F	(-)XMID.C	-0.27	0.027	*
ASYM.F	(-)XMID.F	0.57	0.000	*
ASYM.F	(-)XMID.H	-0.07	0.547	
ASYM.F	(-)TOL_XMID.F	0.61	0.000	*
ASYM.F	(-)TOL_XMID.H	0.40	0.001	*
ASYM.H	TOL_ASYM.F	-0.16	0.195	
ASYM.H	TOL_ASYM.H	0.40	0.001	*
ASYM.H	IGR.C	0.29	0.017	*
ASYM.H	IGR.F	0.31	0.008	*
ASYM.H	IGR.H	-0.22	0.067	
ASYM.H	TOL_IGR.F	0.02	0.848	
ASYM.H	TOL_IGR.H	-0.06	0.626	
ASYM.H	LA.C	0.46	0.000	*
ASYM.H	LA.F	0.01	0.941	
ASYM.H	LA.H	0.71	0.000	*
ASYM.H	LDI.C	0.33	0.006	*
ASYM.H	LDI.F	0.12	0.332	
ASYM.H	LDI.H	0.57	0.000	*
ASYM.H	LDMC.C	0.43	0.000	*
ASYM.H	LDMC.F	0.25	0.035	*
ASYM.H	LDMC.H	0.28	0.020	*
ASYM.H	SSIZ.C	-0.01	0.930	
ASYM.H	LTH.C	-0.27	0.027	*
ASYM.H	LTH.F	-0.34	0.004	*
ASYM.H	LTH.H	0.23	0.054	
ASYM.H	MGR.C	0.42	0.000	*
ASYM.H	MGR.F	0.16	0.183	
ASYM.H	MGR.H	0.03	0.804	
ASYM.H	TOL_MGR.F	-0.01	0.911	
ASYM.H	TOL_MGR.H	-0.08	0.494	
ASYM.H	NLEA.C	-0.03	0.826	
ASYM.H	NLEA.F	-0.03	0.777	
ASYM.H	NLEA.H	0.05	0.704	
ASYM.H	RESmT1.C	-0.23	0.063	

trait_1	trait_2	corr. coeff	*p-value*	
ASYM.H	RESmT2.C	0.22	0.063	
ASYM.H	RESmT2.F	0.18	0.140	
ASYM.H	RESpT1.C	0.04	0.720	
ASYM.H	RESpT2.C	0.55	0.000	*
ASYM.H	RESpT2.H	0.64	0.000	*
ASYM.H	SLA.C	-0.14	0.249	
ASYM.H	SLA.F	0.00	0.999	
ASYM.H	SLA.H	-0.12	0.324	
ASYM.H	TGER.C	-0.16	0.199	
ASYM.H	(-)XMID.C	-0.12	0.339	
ASYM.H	(-)XMID.F	0.08	0.531	
ASYM.H	(-)XMID.H	0.30	0.012	*
ASYM.H	(-)TOL_XMID.F	0.14	0.243	
ASYM.H	(-)TOL_XMID.H	0.37	0.002	*
TOL_ASYM.F	TOL_ASYM.H	-0.09	0.448	
TOL_ASYM.F	IGR.C	0.13	0.273	
TOL_ASYM.F	IGR.F	-0.43	0.000	*
TOL_ASYM.F	IGR.H	-0.28	0.019	*
TOL_ASYM.F	TOL_IGR.F	-0.46	0.000	*
TOL_ASYM.F	TOL_IGR.H	-0.20	0.096	
TOL_ASYM.F	LA.C	-0.07	0.553	
TOL_ASYM.F	LA.F	-0.08	0.535	
TOL_ASYM.F	LA.H	-0.41	0.001	*
TOL_ASYM.F	LDI.C	0.27	0.027	*
TOL_ASYM.F	LDI.F	0.22	0.070	
TOL_ASYM.F	LDI.H	0.16	0.183	
TOL_ASYM.F	LDMC.C	-0.11	0.388	
TOL_ASYM.F	LDMC.F	-0.42	0.000	*
TOL_ASYM.F	LDMC.H	0.12	0.330	
TOL_ASYM.F	SSIZ.C	0.09	0.468	
TOL_ASYM.F	LTH.C	0.35	0.003	*
TOL_ASYM.F	LTH.F	0.24	0.051	
TOL_ASYM.F	LTH.H	-0.07	0.593	
TOL_ASYM.F	MGR.C	0.10	0.429	
TOL_ASYM.F	MGR.F	-0.05	0.704	
TOL_ASYM.F	MGR.H	-0.06	0.650	
TOL_ASYM.F	TOL_MGR.F	-0.14	0.260	
TOL_ASYM.F	TOL_MGR.H	0.15	0.224	
TOL_ASYM.F	NLEA.C	0.09	0.471	
TOL_ASYM.F	NLEA.F	0.17	0.172	
TOL_ASYM.F	NLEA.H	-0.01	0.913	
TOL_ASYM.F	RESmT1.C	0.09	0.471	
TOL_ASYM.F	RESmT2.C	-0.20	0.108	
TOL_ASYM.F	RESmT2.F	0.06	0.623	
TOL_ASYM.F	RESpT1.C	-0.29	0.017	*
TOL_ASYM.F	RESpT2.C	-0.17	0.172	
TOL_ASYM.F	RESpT2.H	-0.44	0.000	*
TOL_ASYM.F	SLA.C	0.00	0.969	
TOL_ASYM.F	SLA.F	0.06	0.638	
TOL_ASYM.F	SLA.H	-0.06	0.644	
TOL_ASYM.F	TGER.C	-0.28	0.022	*
TOL_ASYM.F	(-)XMID.C	-0.50	0.000	*
TOL_ASYM.F	(-)XMID.F	0.64	0.000	*
TOL_ASYM.F	(-)XMID.H	-0.19	0.111	
TOL_ASYM.F	(-)TOL_XMID.F	0.81	0.000	*
TOL_ASYM.F	(-)TOL_XMID.H	0.30	0.013	*
TOL_ASYM.H	IGR.C	0.41	0.000	*
TOL_ASYM.H	IGR.F	0.41	0.000	*
TOL_ASYM.H	IGR.H	-0.02	0.852	
TOL_ASYM.H	TOL_IGR.F	-0.03	0.838	
TOL_ASYM.H	TOL_IGR.H	0.09	0.441	
TOL_ASYM.H	LA.C	0.10	0.403	
TOL_ASYM.H	LA.F	-0.07	0.555	
TOL_ASYM.H	LA.H	0.32	0.008	*
TOL_ASYM.H	LDI.C	0.32	0.008	*

trait_1	trait_2	corr. coeff	*p-value*	
TOL_ASYM.H	LDI.F	0.16	0.177	
TOL_ASYM.H	LDI.H	0.38	0.001	*
TOL_ASYM.H	LDMC.C	0.08	0.538	
TOL_ASYM.H	LDMC.F	0.09	0.481	
TOL_ASYM.H	LDMC.H	-0.04	0.717	
TOL_ASYM.H	SSIZ.C	-0.17	0.175	
TOL_ASYM.H	LTH.C	-0.16	0.197	
TOL_ASYM.H	LTH.F	-0.22	0.070	
TOL_ASYM.H	LTH.H	-0.12	0.320	
TOL_ASYM.H	MGR.C	0.46	0.000	*
TOL_ASYM.H	MGR.F	0.06	0.637	
TOL_ASYM.H	MGR.H	-0.01	0.928	
TOL_ASYM.H	TOL_MGR.F	-0.13	0.298	
TOL_ASYM.H	TOL_MGR.H	-0.08	0.530	
TOL_ASYM.H	NLEA.C	0.15	0.209	
TOL_ASYM.H	NLEA.F	0.07	0.583	
TOL_ASYM.H	NLEA.H	0.21	0.079	
TOL_ASYM.H	RESmT1.C	0.00	0.992	
TOL_ASYM.H	RESmT2.C	0.36	0.002	*
TOL_ASYM.H	RESmT2.F	-0.16	0.182	
TOL_ASYM.H	RESpT1.C	0.07	0.551	
TOL_ASYM.H	RESpT2.C	0.28	0.018	*
TOL_ASYM.H	RESpT2.H	0.33	0.005	*
TOL_ASYM.H	SLA.C	0.02	0.900	
TOL_ASYM.H	SLA.F	0.13	0.296	
TOL_ASYM.H	SLA.H	0.08	0.509	
TOL_ASYM.H	TGER.C	-0.36	0.002	*
TOL_ASYM.H	(-)XMID.C	-0.08	0.518	
TOL_ASYM.H	(-)XMID.F	0.03	0.813	
TOL_ASYM.H	(-)XMID.H	0.28	0.019	*
TOL_ASYM.H	(-)TOL_XMID.F	0.05	0.713	
TOL_ASYM.H	(-)TOL_XMID.H	0.17	0.162	
IGR.C	IGR.F	0.19	0.111	
IGR.C	IGR.H	0.10	0.430	
IGR.C	TOL_IGR.F	-0.67	0.000	*
IGR.C	TOL_IGR.H	0.40	0.001	*
IGR.C	LA.C	0.14	0.245	
IGR.C	LA.F	0.14	0.237	
IGR.C	LA.H	0.27	0.023	*
IGR.C	LDI.C	0.12	0.328	
IGR.C	LDI.F	0.09	0.484	
IGR.C	LDI.H	0.09	0.477	
IGR.C	LDMC.C	0.00	0.989	
IGR.C	LDMC.F	-0.35	0.003	*
IGR.C	LDMC.H	-0.38	0.001	*
IGR.C	SSIZ.C	-0.07	0.567	
IGR.C	LTH.C	0.12	0.336	
IGR.C	LTH.F	0.25	0.039	*
IGR.C	LTH.H	-0.08	0.512	
IGR.C	MGR.C	0.27	0.024	*
IGR.C	MGR.F	-0.29	0.017	*
IGR.C	MGR.H	-0.09	0.470	
IGR.C	TOL_MGR.F	-0.38	0.001	*
IGR.C	TOL_MGR.H	0.15	0.225	
IGR.C	NLEA.C	0.29	0.016	*
IGR.C	NLEA.F	0.18	0.142	
IGR.C	NLEA.H	0.29	0.016	*
IGR.C	RESmT1.C	0.17	0.150	
IGR.C	RESmT2.C	0.42	0.000	*
IGR.C	RESmT2.F	0.35	0.003	*
IGR.C	RESpT1.C	0.36	0.003	*
IGR.C	RESpT2.C	0.00	0.980	
IGR.C	RESpT2.H	0.22	0.067	
IGR.C	SLA.C	-0.15	0.212	
IGR.C	SLA.F	0.38	0.001	*

trait_1	trait_2	corr. coeff	*p-value*	
IGR.C	SLA.H	0.25	0.036	*
IGR.C	TGER.C	-0.56	0.000	*
IGR.C	(-)XMID.C	-0.19	0.113	
IGR.C	(-)XMID.F	0.22	0.070	
IGR.C	(-)XMID.H	0.57	0.000	*
IGR.C	(-)TOL_XMID.F	0.23	0.056	
IGR.C	(-)TOL_XMID.H	0.12	0.311	
IGR.F	IGR.H	0.22	0.075	
IGR.F	TOL_IGR.F	0.57	0.000	*
IGR.F	TOL_IGR.H	0.19	0.109	
IGR.F	LA.C	0.23	0.058	
IGR.F	LA.F	0.23	0.061	
IGR.F	LA.H	0.57	0.000	*
IGR.F	LDI.C	-0.06	0.638	
IGR.F	LDI.F	0.04	0.726	
IGR.F	LDI.H	0.09	0.483	
IGR.F	LDMC.C	0.05	0.703	
IGR.F	LDMC.F	0.30	0.013	*
IGR.F	LDMC.H	-0.24	0.044	*
IGR.F	SSIZ.C	-0.26	0.032	*
IGR.F	LTH.C	-0.33	0.006	*
IGR.F	LTH.F	-0.55	0.000	*
IGR.F	LTH.H	-0.11	0.376	
IGR.F	MGR.C	-0.12	0.345	
IGR.F	MGR.F	0.26	0.030	*
IGR.F	MGR.H	0.07	0.559	
IGR.F	TOL_MGR.F	0.26	0.028	*
IGR.F	TOL_MGR.H	-0.24	0.049	*
IGR.F	NLEA.C	0.11	0.364	
IGR.F	NLEA.F	-0.02	0.889	
IGR.F	NLEA.H	0.22	0.075	
IGR.F	RESmT1.C	0.26	0.033	*
IGR.F	RESmT2.C	0.33	0.005	*
IGR.F	RESmT2.F	-0.16	0.199	
IGR.F	RESpT1.C	0.21	0.078	
IGR.F	RESpT2.C	0.42	0.000	*
IGR.F	RESpT2.H	0.48	0.000	*
IGR.F	SLA.C	0.20	0.093	
IGR.F	SLA.F	0.16	0.196	
IGR.F	SLA.H	0.35	0.004	*
IGR.F	TGER.C	-0.07	0.577	
IGR.F	(-)XMID.C	0.08	0.521	
IGR.F	(-)XMID.F	-0.37	0.002	*
IGR.F	(-)XMID.H	0.55	0.000	*
IGR.F	(-)TOL_XMID.F	-0.35	0.003	*
IGR.F	(-)TOL_XMID.H	-0.08	0.491	
IGR.H	TOL_IGR.F	0.10	0.422	
IGR.H	TOL_IGR.H	0.81	0.000	*
IGR.H	LA.C	0.05	0.677	
IGR.H	LA.F	0.17	0.161	
IGR.H	LA.H	-0.03	0.776	
IGR.H	LDI.C	-0.14	0.261	
IGR.H	LDI.F	0.09	0.462	
IGR.H	LDI.H	-0.23	0.061	
IGR.H	LDMC.C	0.04	0.770	
IGR.H	LDMC.F	-0.18	0.129	
IGR.H	LDMC.H	-0.24	0.044	*
IGR.H	SSIZ.C	-0.21	0.081	
IGR.H	LTH.C	0.11	0.359	
IGR.H	LTH.F	0.10	0.392	
IGR.H	LTH.H	-0.44	0.000	*
IGR.H	MGR.C	-0.30	0.013	*
IGR.H	MGR.F	-0.11	0.364	
IGR.H	MGR.H	-0.13	0.273	
IGR.H	TOL_MGR.F	-0.01	0.959	
IGR.H	TOL_MGR.H	0.01	0.960	
IGR.H	NLEA.C	0.13	0.277	
IGR.H	NLEA.F	0.02	0.861	
IGR.H	NLEA.H	0.02	0.899	
IGR.H	RESmT1.C	0.21	0.085	
IGR.H	RESmT2.C	0.48	0.000	*
IGR.H	RESmT2.F	0.15	0.234	
IGR.H	RESpT1.C	0.53	0.000	*
IGR.H	RESpT2.C	-0.19	0.125	
IGR.H	RESpT2.H	-0.09	0.455	
IGR.H	SLA.C	-0.11	0.364	
IGR.H	SLA.F	0.42	0.000	*
IGR.H	SLA.H	0.29	0.016	*
IGR.H	TGER.C	-0.09	0.477	
IGR.H	(-)XMID.C	0.30	0.012	*
IGR.H	(-)XMID.F	-0.14	0.261	
IGR.H	(-)XMID.H	0.27	0.026	*
IGR.H	(-)TOL_XMID.F	-0.27	0.026	*
IGR.H	(-)TOL_XMID.H	-0.27	0.023	*
TOL_IGR.F	TOL_IGR.H	-0.16	0.193	
TOL_IGR.F	LA.C	0.09	0.485	
TOL_IGR.F	LA.F	0.07	0.595	
TOL_IGR.F	LA.H	0.19	0.120	
TOL_IGR.F	LDI.C	-0.08	0.527	
TOL_IGR.F	LDI.F	0.02	0.897	
TOL_IGR.F	LDI.H	0.03	0.833	
TOL_IGR.F	LDMC.C	0.10	0.401	
TOL_IGR.F	LDMC.F	0.55	0.000	*
TOL_IGR.F	LDMC.H	0.18	0.145	
TOL_IGR.F	SSIZ.C	-0.11	0.359	
TOL_IGR.F	LTH.C	-0.36	0.002	*
TOL_IGR.F	LTH.F	-0.59	0.000	*
TOL_IGR.F	LTH.H	0.03	0.797	
TOL_IGR.F	MGR.C	-0.30	0.013	*
TOL_IGR.F	MGR.F	0.41	0.000	*
TOL_IGR.F	MGR.H	0.11	0.363	
TOL_IGR.F	TOL_MGR.F	0.51	0.000	*
TOL_IGR.F	TOL_MGR.H	-0.29	0.015	*
TOL_IGR.F	NLEA.C	-0.13	0.296	
TOL_IGR.F	NLEA.F	-0.14	0.258	
TOL_IGR.F	NLEA.H	-0.04	0.768	
TOL_IGR.F	RESmT1.C	0.02	0.893	
TOL_IGR.F	RESmT2.C	-0.06	0.613	
TOL_IGR.F	RESmT2.F	-0.37	0.002	*
TOL_IGR.F	RESpT1.C	-0.14	0.252	
TOL_IGR.F	RESpT2.C	0.32	0.007	*
TOL_IGR.F	RESpT2.H	0.19	0.120	
TOL_IGR.F	SLA.C	0.24	0.047	*
TOL_IGR.F	SLA.F	-0.20	0.093	
TOL_IGR.F	SLA.H	0.01	0.950	
TOL_IGR.F	TGER.C	0.39	0.001	*
TOL_IGR.F	(-)XMID.C	0.21	0.076	
TOL_IGR.F	(-)XMID.F	-0.45	0.000	*
TOL_IGR.F	(-)XMID.H	-0.05	0.689	
TOL_IGR.F	(-)TOL_XMID.F	-0.46	0.000	*
TOL_IGR.F	(-)TOL_XMID.H	-0.17	0.169	
TOL_IGR.H	LA.C	-0.02	0.893	
TOL_IGR.H	LA.F	0.05	0.710	
TOL_IGR.H	LA.H	-0.05	0.677	
TOL_IGR.H	LDI.C	0.00	0.972	
TOL_IGR.H	LDI.F	0.15	0.207	
TOL_IGR.H	LDI.H	-0.07	0.587	
TOL_IGR.H	LDMC.C	0.11	0.371	
TOL_IGR.H	LDMC.F	-0.40	0.001	*
TOL_IGR.H	LDMC.H	-0.31	0.009	*

trait_1	trait_2	corr. coeff	*p-value*	
TOL_IGR.H	SSIZ.C	-0.10	0.409	
TOL_IGR.H	LTH.C	0.06	0.624	
TOL_IGR.H	LTH.F	0.18	0.144	
TOL_IGR.H	LTH.H	-0.46	0.000	*
TOL_IGR.H	MGR.C	-0.22	0.066	
TOL_IGR.H	MGR.F	-0.19	0.125	
TOL_IGR.H	MGR.H	-0.09	0.484	
TOL_IGR.H	TOL_MGR.F	-0.11	0.363	
TOL_IGR.H	TOL_MGR.H	0.16	0.202	
TOL_IGR.H	NLEA.C	0.27	0.024	*
TOL_IGR.H	NLEA.F	0.11	0.367	
TOL_IGR.H	NLEA.H	0.18	0.133	
TOL_IGR.H	RESmT1.C	0.12	0.343	
TOL_IGR.H	RESmT2.C	0.50	0.000	*
TOL_IGR.H	RESmT2.F	0.32	0.007	*
TOL_IGR.H	RESpT1.C	0.66	0.000	*
TOL_IGR.H	RESpT2.C	-0.21	0.091	
TOL_IGR.H	RESpT2.H	0.03	0.810	
TOL_IGR.H	SLA.C	-0.18	0.145	
TOL_IGR.H	SLA.F	0.67	0.000	*
TOL_IGR.H	SLA.H	0.34	0.005	*
TOL_IGR.H	TGER.C	-0.26	0.030	*
TOL_IGR.H	(-)XMID.C	0.07	0.545	
TOL_IGR.H	(-)XMID.F	-0.03	0.836	
TOL_IGR.H	(-)XMID.H	0.45	0.000	*
TOL_IGR.H	(-)TOL_XMID.F	-0.07	0.556	
TOL_IGR.H	(-)TOL_XMID.H	-0.25	0.040	*
LA.C	LA.F	0.64	0.000	*
LA.C	LA.H	0.57	0.000	*
LA.C	LDI.C	0.22	0.070	
LA.C	LDI.F	0.26	0.032	*
LA.C	LDI.H	0.23	0.055	
LA.C	LDMC.C	0.12	0.313	
LA.C	LDMC.F	0.24	0.050	
LA.C	LDMC.H	0.07	0.553	
LA.C	SSIZ.C	-0.04	0.759	
LA.C	LTH.C	0.03	0.806	
LA.C	LTH.F	-0.04	0.767	
LA.C	LTH.H	0.17	0.172	
LA.C	MGR.C	0.14	0.246	
LA.C	MGR.F	-0.10	0.408	
LA.C	MGR.H	-0.07	0.557	
LA.C	TOL_MGR.F	-0.13	0.284	
LA.C	TOL_MGR.H	-0.04	0.714	
LA.C	NLEA.C	-0.10	0.392	
LA.C	NLEA.F	-0.08	0.526	
LA.C	NLEA.H	-0.07	0.542	
LA.C	RESmT1.C	0.09	0.466	
LA.C	RESmT2.C	0.10	0.409	
LA.C	RESmT2.F	0.03	0.797	
LA.C	RESpT1.C	-0.02	0.865	
LA.C	RESpT2.C	0.27	0.027	*
LA.C	RESpT2.H	0.14	0.236	
LA.C	SLA.C	-0.11	0.362	
LA.C	SLA.F	-0.19	0.124	
LA.C	SLA.H	-0.23	0.054	
LA.C	TGER.C	-0.16	0.202	
LA.C	(-)XMID.C	-0.02	0.856	
LA.C	(-)XMID.F	-0.05	0.667	
LA.C	(-)XMID.H	0.22	0.066	
LA.C	(-)TOL_XMID.F	-0.05	0.704	
LA.C	(-)TOL_XMID.H	0.31	0.009	*
LA.F	LA.H	0.35	0.004	*
LA.F	LDI.C	-0.13	0.293	
LA.F	LDI.F	0.08	0.496	
LA.F	LDI.H	-0.21	0.083	
LA.F	LDMC.C	-0.16	0.189	
LA.F	LDMC.F	0.13	0.274	
LA.F	LDMC.H	-0.18	0.149	
LA.F	SSIZ.C	-0.04	0.750	
LA.F	LTH.C	0.09	0.438	
LA.F	LTH.F	0.18	0.150	
LA.F	LTH.H	-0.02	0.862	
LA.F	MGR.C	-0.07	0.578	
LA.F	MGR.F	-0.01	0.958	
LA.F	MGR.H	-0.07	0.588	
LA.F	TOL_MGR.F	0.01	0.964	
LA.F	TOL_MGR.H	0.00	0.989	
LA.F	NLEA.C	-0.11	0.377	
LA.F	NLEA.F	-0.07	0.560	
LA.F	NLEA.H	-0.07	0.550	
LA.F	RESmT1.C	0.36	0.002	*
LA.F	RESmT2.C	0.07	0.563	
LA.F	RESmT2.F	-0.08	0.505	
LA.F	RESpT1.C	0.04	0.719	
LA.F	RESpT2.C	0.02	0.860	
LA.F	RESpT2.H	-0.05	0.662	
LA.F	SLA.C	0.02	0.859	
LA.F	SLA.F	-0.23	0.056	
LA.F	SLA.H	-0.04	0.765	
LA.F	TGER.C	-0.01	0.912	
LA.F	(-)XMID.C	0.05	0.683	
LA.F	(-)XMID.F	-0.17	0.171	
LA.F	(-)XMID.H	0.29	0.016	*
LA.F	(-)TOL_XMID.F	-0.21	0.090	
LA.F	(-)TOL_XMID.H	0.09	0.454	
LA.H	LDI.C	-0.08	0.530	
LA.H	LDI.F	-0.15	0.222	
LA.H	LDI.H	0.16	0.189	
LA.H	LDMC.C	0.16	0.193	
LA.H	LDMC.F	0.39	0.001	*
LA.H	LDMC.H	-0.06	0.622	
LA.H	SSIZ.C	-0.13	0.274	
LA.H	LTH.C	-0.26	0.029	*
LA.H	LTH.F	-0.46	0.000	*
LA.H	LTH.H	0.09	0.456	
LA.H	MGR.C	0.25	0.042	*
LA.H	MGR.F	0.09	0.485	
LA.H	MGR.H	-0.01	0.918	
LA.H	TOL_MGR.F	0.00	0.976	
LA.H	TOL_MGR.H	-0.26	0.029	*
LA.H	NLEA.C	-0.09	0.442	
LA.H	NLEA.F	-0.10	0.394	
LA.H	NLEA.H	-0.02	0.878	
LA.H	RESmT1.C	0.02	0.901	
LA.H	RESmT2.C	0.27	0.026	*
LA.H	RESmT2.F	-0.07	0.564	
LA.H	RESpT1.C	0.13	0.285	
LA.H	RESpT2.C	0.52	0.000	*
LA.H	RESpT2.H	0.75	0.000	*
LA.H	SLA.C	0.09	0.470	
LA.H	SLA.F	-0.08	0.534	
LA.H	SLA.H	0.18	0.130	
LA.H	TGER.C	-0.02	0.850	
LA.H	(-)XMID.C	0.06	0.614	
LA.H	(-)XMID.F	-0.29	0.015	*
LA.H	(-)XMID.H	0.31	0.010	*
LA.H	(-)TOL_XMID.F	-0.24	0.045	*
LA.H	(-)TOL_XMID.H	0.15	0.207	
LDI.C	LDI.F	0.81	0.000	*

trait_1	trait_2	corr. coeff	*p-value*	
LDI.C	LDI.H	0.83	0.000	*
LDI.C	LDMC.C	0.12	0.342	
LDI.C	LDMC.F	-0.12	0.313	
LDI.C	LDMC.H	0.17	0.158	
LDI.C	SSIZ.C	0.07	0.572	
LDI.C	LTH.C	-0.09	0.466	
LDI.C	LTH.F	-0.02	0.866	
LDI.C	LTH.H	0.16	0.183	
LDI.C	MGR.C	0.28	0.021	*
LDI.C	MGR.F	-0.09	0.448	
LDI.C	MGR.H	0.21	0.088	
LDI.C	TOL_MGR.F	-0.17	0.152	
LDI.C	TOL_MGR.H	0.32	0.007	*
LDI.C	NLEA.C	0.12	0.322	
LDI.C	NLEA.F	0.12	0.336	
LDI.C	NLEA.H	0.12	0.332	
LDI.C	RESmT1.C	-0.11	0.354	
LDI.C	RESmT2.C	0.03	0.838	
LDI.C	RESmT2.F	0.23	0.061	
LDI.C	RESpT1.C	-0.15	0.222	
LDI.C	RESpT2.C	0.18	0.135	
LDI.C	RESpT2.H	0.01	0.943	
LDI.C	SLA.C	-0.07	0.541	
LDI.C	SLA.F	0.13	0.278	
LDI.C	SLA.H	-0.25	0.037	*
LDI.C	TGER.C	-0.26	0.032	*
LDI.C	(-)XMID.C	-0.16	0.203	
LDI.C	(-)XMID.F	0.37	0.002	*
LDI.C	(-)XMID.H	0.09	0.485	
LDI.C	(-)TOL_XMID.F	0.33	0.006	*
LDI.C	(-)TOL_XMID.H	0.35	0.003	*
LDI.F	LDI.H	0.68	0.000	*
LDI.F	LDMC.C	0.13	0.271	
LDI.F	LDMC.F	-0.07	0.594	
LDI.F	LDMC.H	0.01	0.923	
LDI.F	SSIZ.C	0.03	0.837	
LDI.F	LTH.C	0.09	0.482	
LDI.F	LTH.F	0.08	0.488	
LDI.F	LTH.H	0.13	0.296	
LDI.F	MGR.C	0.08	0.503	
LDI.F	MGR.F	-0.15	0.231	
LDI.F	MGR.H	0.12	0.338	
LDI.F	TOL_MGR.F	-0.19	0.110	
LDI.F	TOL_MGR.H	0.28	0.019	*
LDI.F	NLEA.C	0.11	0.372	
LDI.F	NLEA.F	0.13	0.295	
LDI.F	NLEA.H	0.11	0.353	
LDI.F	RESmT1.C	0.13	0.286	
LDI.F	RESmT2.C	0.04	0.725	
LDI.F	RESmT2.F	0.29	0.017	*
LDI.F	RESpT1.C	-0.04	0.718	
LDI.F	RESpT2.C	0.25	0.037	*
LDI.F	RESpT2.H	-0.16	0.201	
LDI.F	SLA.C	-0.16	0.198	
LDI.F	SLA.F	0.08	0.493	
LDI.F	SLA.H	-0.19	0.115	
LDI.F	TGER.C	-0.37	0.002	*
LDI.F	(-)XMID.C	-0.08	0.539	
LDI.F	(-)XMID.F	0.20	0.101	
LDI.F	(-)XMID.H	0.31	0.010	*
LDI.F	(-)TOL_XMID.F	0.12	0.336	
LDI.F	(-)TOL_XMID.H	0.22	0.073	
LDI.H	LDMC.C	0.29	0.017	*
LDI.H	LDMC.F	0.03	0.822	
LDI.H	LDMC.H	0.18	0.137	
LDI.H	SSIZ.C	0.00	0.982	
LDI.H	LTH.C	-0.15	0.223	
LDI.H	LTH.F	-0.22	0.066	
LDI.H	LTH.H	0.07	0.586	
LDI.H	MGR.C	0.27	0.023	*
LDI.H	MGR.F	0.08	0.522	
LDI.H	MGR.H	0.18	0.134	
LDI.H	TOL_MGR.F	-0.04	0.750	
LDI.H	TOL_MGR.H	0.14	0.247	
LDI.H	NLEA.C	0.12	0.327	
LDI.H	NLEA.F	0.11	0.375	
LDI.H	NLEA.H	0.12	0.321	
LDI.H	RESmT1.C	-0.12	0.319	
LDI.H	RESmT2.C	0.08	0.526	
LDI.H	RESmT2.F	0.17	0.175	
LDI.H	RESpT1.C	-0.08	0.515	
LDI.H	RESpT2.C	0.36	0.002	*
LDI.H	RESpT2.H	0.23	0.054	
LDI.H	SLA.C	-0.13	0.288	
LDI.H	SLA.F	0.13	0.270	
LDI.H	SLA.H	-0.08	0.501	
LDI.H	TGER.C	-0.27	0.022	*
LDI.H	(-)XMID.C	-0.20	0.096	
LDI.H	(-)XMID.F	0.29	0.016	*
LDI.H	(-)XMID.H	0.15	0.226	
LDI.H	(-)TOL_XMID.F	0.33	0.005	*
LDI.H	(-)TOL_XMID.H	0.34	0.004	*
LDMC.C	LDMC.F	0.41	0.000	*
LDMC.C	LDMC.H	0.56	0.000	*
LDMC.C	SSIZ.C	0.11	0.367	
LDMC.C	LTH.C	-0.01	0.946	
LDMC.C	LTH.F	-0.20	0.105	
LDMC.C	LTH.H	0.11	0.366	
LDMC.C	MGR.C	-0.06	0.636	
LDMC.C	MGR.F	0.16	0.185	
LDMC.C	MGR.H	-0.06	0.642	
LDMC.C	TOL_MGR.F	0.19	0.112	
LDMC.C	TOL_MGR.H	-0.13	0.300	
LDMC.C	NLEA.C	-0.01	0.932	
LDMC.C	NLEA.F	0.06	0.629	
LDMC.C	NLEA.H	0.06	0.631	
LDMC.C	RESmT1.C	-0.11	0.375	
LDMC.C	RESmT2.C	0.25	0.039	*
LDMC.C	RESmT2.F	0.14	0.239	
LDMC.C	RESpT1.C	0.15	0.217	
LDMC.C	RESpT2.C	0.20	0.105	
LDMC.C	RESpT2.H	0.28	0.019	*
LDMC.C	SLA.C	-0.48	0.000	*
LDMC.C	SLA.F	0.01	0.945	
LDMC.C	SLA.H	-0.13	0.299	
LDMC.C	TGER.C	-0.14	0.264	
LDMC.C	(-)XMID.C	-0.27	0.023	*
LDMC.C	(-)XMID.F	-0.18	0.142	
LDMC.C	(-)XMID.H	0.06	0.617	
LDMC.C	(-)TOL_XMID.F	0.03	0.838	
LDMC.C	(-)TOL_XMID.H	-0.01	0.942	
LDMC.F	LDMC.H	0.34	0.004	*
LDMC.F	SSIZ.C	-0.06	0.620	
LDMC.F	LTH.C	-0.30	0.012	*
LDMC.F	LTH.F	-0.41	0.000	*
LDMC.F	LTH.H	0.40	0.001	*
LDMC.F	MGR.C	0.04	0.725	
LDMC.F	MGR.F	0.25	0.041	*
LDMC.F	MGR.H	0.03	0.782	
LDMC.F	TOL_MGR.F	0.30	0.011	*

trait_1	trait_2	corr. coeff	*p-value*	
LDMC.F	TOL_MGR.H	-0.28	0.019	*
LDMC.F	NLEA.C	-0.08	0.526	
LDMC.F	NLEA.F	0.04	0.735	
LDMC.F	NLEA.H	0.06	0.630	
LDMC.F	RESmT1.C	-0.06	0.626	
LDMC.F	RESmT2.C	-0.09	0.446	
LDMC.F	RESmT2.F	-0.27	0.023	*
LDMC.F	RESpT1.C	-0.33	0.006	*
LDMC.F	RESpT2.C	0.37	0.002	*
LDMC.F	RESpT2.H	0.30	0.013	*
LDMC.F	SLA.C	0.06	0.618	
LDMC.F	SLA.F	-0.65	0.000	*
LDMC.F	SLA.H	-0.14	0.243	
LDMC.F	TGER.C	0.12	0.321	
LDMC.F	(-)XMID.C	0.09	0.487	
LDMC.F	(-)XMID.F	-0.55	0.000	*
LDMC.F	(-)XMID.H	0.02	0.864	
LDMC.F	(-)TOL_XMID.F	-0.49	0.000	*
LDMC.F	(-)TOL_XMID.H	0.04	0.728	
LDMC.H	SSIZ.C	0.16	0.196	
LDMC.H	LTH.C	-0.14	0.254	
LDMC.H	LTH.F	-0.24	0.048	*
LDMC.H	LTH.H	0.20	0.101	
LDMC.H	MGR.C	0.11	0.355	
LDMC.H	MGR.F	0.36	0.002	*
LDMC.H	MGR.H	-0.01	0.967	
LDMC.H	TOL_MGR.F	0.32	0.008	*
LDMC.H	TOL_MGR.H	-0.09	0.471	
LDMC.H	NLEA.C	-0.29	0.017	*
LDMC.H	NLEA.F	-0.14	0.237	
LDMC.H	NLEA.H	-0.25	0.040	*
LDMC.H	RESmT1.C	-0.42	0.000	*
LDMC.H	RESmT2.C	-0.11	0.352	
LDMC.H	RESmT2.F	-0.15	0.231	
LDMC.H	RESpT1.C	-0.25	0.039	*
LDMC.H	RESpT2.C	0.11	0.367	
LDMC.H	RESpT2.H	0.05	0.706	
LDMC.H	SLA.C	-0.09	0.443	
LDMC.H	SLA.F	-0.20	0.095	
LDMC.H	SLA.H	-0.54	0.000	*
LDMC.H	TGER.C	0.19	0.127	
LDMC.H	(-)XMID.C	-0.09	0.444	
LDMC.H	(-)XMID.F	0.10	0.424	
LDMC.H	(-)XMID.H	-0.31	0.010	*
LDMC.H	(-)TOL_XMID.F	0.16	0.185	
LDMC.H	(-)TOL_XMID.H	0.32	0.008	*
SSIZ.C	LTH.C	0.16	0.183	
SSIZ.C	LTH.F	0.07	0.577	
SSIZ.C	LTH.H	0.09	0.474	
SSIZ.C	MGR.C	0.12	0.343	
SSIZ.C	MGR.F	-0.11	0.359	
SSIZ.C	MGR.H	0.16	0.183	
SSIZ.C	TOL_MGR.F	-0.13	0.289	
SSIZ.C	TOL_MGR.H	0.24	0.048	*
SSIZ.C	NLEA.C	-0.18	0.146	
SSIZ.C	NLEA.F	-0.12	0.322	
SSIZ.C	NLEA.H	-0.11	0.361	
SSIZ.C	RESmT1.C	-0.05	0.680	
SSIZ.C	RESmT2.C	-0.12	0.307	
SSIZ.C	RESmT2.F	0.27	0.023	*
SSIZ.C	RESpT1.C	-0.04	0.729	
SSIZ.C	RESpT2.C	-0.01	0.920	
SSIZ.C	RESpT2.H	0.05	0.663	
SSIZ.C	SLA.C	-0.24	0.043	*
SSIZ.C	SLA.F	-0.21	0.089	

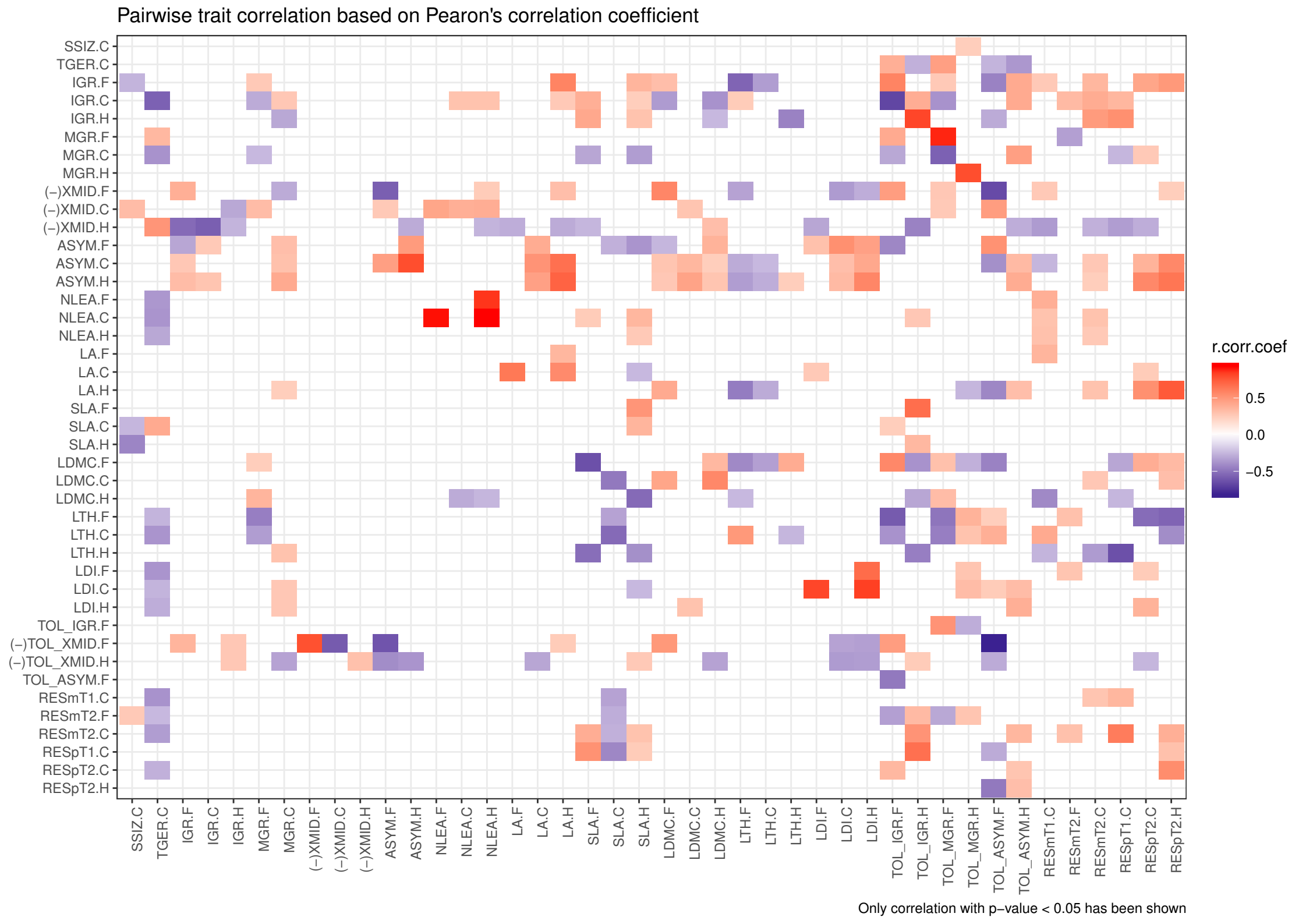
trait_1	trait_2	corr. coeff	*p-value*	
SSIZ.C	SLA.H	-0.43	0.000	*
SSIZ.C	TGER.C	0.13	0.277	
SSIZ.C	(-)XMID.C	-0.33	0.006	*
SSIZ.C	(-)XMID.F	0.00	0.996	
SSIZ.C	(-)XMID.H	-0.19	0.126	
SSIZ.C	(-)TOL_XMID.F	0.15	0.219	
SSIZ.C	(-)TOL_XMID.H	0.11	0.359	
LTH.C	LTH.F	0.49	0.000	*
LTH.C	LTH.H	-0.23	0.052	
LTH.C	MGR.C	0.14	0.261	
LTH.C	MGR.F	-0.36	0.003	*
LTH.C	MGR.H	0.00	0.974	
LTH.C	TOL_MGR.F	-0.46	0.000	*
LTH.C	TOL_MGR.H	0.31	0.010	*
LTH.C	NLEA.C	-0.08	0.523	
LTH.C	NLEA.F	0.01	0.965	
LTH.C	NLEA.H	-0.15	0.220	
LTH.C	RESmT1.C	0.43	0.000	*
LTH.C	RESmT2.C	-0.09	0.438	
LTH.C	RESmT2.F	0.10	0.417	
LTH.C	RESpT1.C	0.19	0.108	
LTH.C	RESpT2.C	-0.07	0.584	
LTH.C	RESpT2.H	-0.37	0.002	*
LTH.C	SLA.C	-0.54	0.000	*
LTH.C	SLA.F	-0.15	0.214	
LTH.C	SLA.H	-0.19	0.123	
LTH.C	TGER.C	-0.40	0.001	*
LTH.C	(-)XMID.C	0.00	0.981	
LTH.C	(-)XMID.F	0.20	0.104	
LTH.C	(-)XMID.H	-0.06	0.650	
LTH.C	(-)TOL_XMID.F	0.13	0.294	
LTH.C	(-)TOL_XMID.H	-0.05	0.699	
LTH.F	LTH.H	0.08	0.528	
LTH.F	MGR.C	0.16	0.185	
LTH.F	MGR.F	-0.46	0.000	*
LTH.F	MGR.H	-0.10	0.424	
LTH.F	TOL_MGR.F	-0.49	0.000	*
LTH.F	TOL_MGR.H	0.38	0.001	*
LTH.F	NLEA.C	0.02	0.863	
LTH.F	NLEA.F	-0.01	0.949	
LTH.F	NLEA.H	-0.11	0.353	
LTH.F	RESmT1.C	0.09	0.484	
LTH.F	RESmT2.C	-0.15	0.220	
LTH.F	RESmT2.F	0.32	0.008	*
LTH.F	RESpT1.C	0.01	0.942	
LTH.F	RESpT2.C	-0.52	0.000	*
LTH.F	RESpT2.H	-0.56	0.000	*
LTH.F	SLA.C	-0.32	0.007	*
LTH.F	SLA.F	-0.05	0.693	
LTH.F	SLA.H	-0.23	0.058	
LTH.F	TGER.C	-0.26	0.028	*
LTH.F	(-)XMID.C	0.06	0.643	
LTH.F	(-)XMID.F	0.32	0.007	*
LTH.F	(-)XMID.H	-0.01	0.911	
LTH.F	(-)TOL_XMID.F	0.16	0.177	
LTH.F	(-)TOL_XMID.H	-0.16	0.189	
LTH.H	MGR.C	0.29	0.016	*
LTH.H	MGR.F	0.03	0.789	
LTH.H	MGR.H	0.23	0.062	
LTH.H	TOL_MGR.F	-0.04	0.764	
LTH.H	TOL_MGR.H	0.16	0.190	
LTH.H	NLEA.C	-0.07	0.593	
LTH.H	NLEA.F	0.04	0.733	
LTH.H	NLEA.H	0.03	0.803	
LTH.H	RESmT1.C	-0.26	0.030	*

trait_1	trait_2	corr. coeff	*p-value*	
LTH.H	RESmT2.C	-0.37	0.002	*
LTH.H	RESmT2.F	0.14	0.238	
LTH.H	RESpT1.C	-0.64	0.000	*
LTH.H	RESpT2.C	0.18	0.133	
LTH.H	RESpT2.H	0.00	0.985	
LTH.H	SLA.C	0.07	0.562	
LTH.H	SLA.F	-0.51	0.000	*
LTH.H	SLA.H	-0.41	0.000	*
LTH.H	TGER.C	0.09	0.486	
LTH.H	(-)XMID.C	-0.08	0.521	
LTH.H	(-)XMID.F	-0.09	0.475	
LTH.H	(-)XMID.H	-0.07	0.559	
LTH.H	(-)TOL_XMID.F	-0.10	0.411	
LTH.H	(-)TOL_XMID.H	0.10	0.425	
MGR.C	MGR.F	-0.24	0.045	*
MGR.C	MGR.H	0.01	0.954	
MGR.C	TOL_MGR.F	-0.56	0.000	*
MGR.C	TOL_MGR.H	0.13	0.284	
MGR.C	NLEA.C	-0.13	0.275	
MGR.C	NLEA.F	-0.08	0.529	
MGR.C	NLEA.H	-0.14	0.240	
MGR.C	RESmT1.C	-0.16	0.182	
MGR.C	RESmT2.C	-0.10	0.396	
MGR.C	RESmT2.F	0.02	0.900	
MGR.C	RESpT1.C	-0.25	0.042	*
MGR.C	RESpT2.C	0.27	0.027	*
MGR.C	RESpT2.H	0.17	0.164	
MGR.C	SLA.C	-0.10	0.423	
MGR.C	SLA.F	-0.31	0.010	*
MGR.C	SLA.H	-0.34	0.005	*
MGR.C	TGER.C	-0.38	0.001	*
MGR.C	(-)XMID.C	0.10	0.432	
MGR.C	(-)XMID.F	0.29	0.014	*
MGR.C	(-)XMID.H	0.06	0.643	
MGR.C	(-)TOL_XMID.F	0.13	0.280	
MGR.C	(-)TOL_XMID.H	0.32	0.008	*
MGR.F	MGR.H	0.24	0.051	
MGR.F	TOL_MGR.F	0.89	0.000	*
MGR.F	TOL_MGR.H	-0.11	0.385	
MGR.F	NLEA.C	0.15	0.219	
MGR.F	NLEA.F	0.23	0.058	
MGR.F	NLEA.H	0.14	0.266	
MGR.F	RESmT1.C	-0.05	0.700	
MGR.F	RESmT2.C	0.09	0.468	
MGR.F	RESmT2.F	-0.33	0.006	*
MGR.F	RESpT1.C	-0.22	0.063	
MGR.F	RESpT2.C	0.12	0.306	
MGR.F	RESpT2.H	0.11	0.357	
MGR.F	SLA.C	0.13	0.285	
MGR.F	SLA.F	-0.04	0.722	
MGR.F	SLA.H	0.07	0.565	
MGR.F	TGER.C	0.34	0.005	*
MGR.F	(-)XMID.C	-0.32	0.007	*
MGR.F	(-)XMID.F	-0.17	0.169	
MGR.F	(-)XMID.H	-0.12	0.321	
MGR.F	(-)TOL_XMID.F	0.10	0.399	
MGR.F	(-)TOL_XMID.H	0.05	0.670	
MGR.H	TOL_MGR.F	0.20	0.107	
MGR.H	TOL_MGR.H	0.80	0.000	*
MGR.H	NLEA.C	0.02	0.902	
MGR.H	NLEA.F	0.05	0.682	
MGR.H	NLEA.H	0.04	0.774	
MGR.H	RESmT1.C	0.02	0.884	
MGR.H	RESmT2.C	-0.11	0.373	
MGR.H	RESmT2.F	0.01	0.950	
MGR.H	RESpT1.C	-0.22	0.064	
MGR.H	RESpT2.C	0.08	0.519	
MGR.H	RESpT2.H	0.16	0.178	
MGR.H	SLA.C	0.07	0.559	
MGR.H	SLA.F	-0.12	0.326	
MGR.H	SLA.H	-0.13	0.276	
MGR.H	TGER.C	0.12	0.338	
MGR.H	(-)XMID.C	-0.03	0.783	
MGR.H	(-)XMID.F	0.04	0.736	
MGR.H	(-)XMID.H	0.04	0.722	
MGR.H	(-)TOL_XMID.F	-0.01	0.920	
MGR.H	(-)TOL_XMID.H	-0.03	0.831	
TOL_MGR.F	TOL_MGR.H	-0.19	0.123	
TOL_MGR.F	NLEA.C	0.11	0.369	
TOL_MGR.F	NLEA.F	0.16	0.199	
TOL_MGR.F	NLEA.H	0.12	0.325	
TOL_MGR.F	RESmT1.C	-0.07	0.563	
TOL_MGR.F	RESmT2.C	0.13	0.280	
TOL_MGR.F	RESmT2.F	-0.30	0.012	*
TOL_MGR.F	RESpT1.C	-0.15	0.230	
TOL_MGR.F	RESpT2.C	-0.04	0.724	
TOL_MGR.F	RESpT2.H	0.08	0.539	
TOL_MGR.F	SLA.C	0.22	0.072	
TOL_MGR.F	SLA.F	0.04	0.760	
TOL_MGR.F	SLA.H	0.17	0.170	
TOL_MGR.F	TGER.C	0.46	0.000	*
TOL_MGR.F	(-)XMID.C	-0.26	0.034	*
TOL_MGR.F	(-)XMID.F	-0.28	0.022	*
TOL_MGR.F	(-)XMID.H	-0.14	0.235	
TOL_MGR.F	(-)TOL_XMID.F	-0.01	0.947	
TOL_MGR.F	(-)TOL_XMID.H	-0.07	0.592	
TOL_MGR.H	NLEA.C	0.09	0.455	
TOL_MGR.H	NLEA.F	0.09	0.460	
TOL_MGR.H	NLEA.H	0.05	0.710	
TOL_MGR.H	RESmT1.C	0.04	0.761	
TOL_MGR.H	RESmT2.C	-0.13	0.282	
TOL_MGR.H	RESmT2.F	0.28	0.020	*
TOL_MGR.H	RESpT1.C	-0.10	0.435	
TOL_MGR.H	RESpT2.C	-0.13	0.287	
TOL_MGR.H	RESpT2.H	-0.13	0.305	
TOL_MGR.H	SLA.C	-0.09	0.456	
TOL_MGR.H	SLA.F	0.00	0.989	
TOL_MGR.H	SLA.H	-0.24	0.049	*
TOL_MGR.H	TGER.C	-0.11	0.374	
TOL_MGR.H	(-)XMID.C	-0.03	0.821	
TOL_MGR.H	(-)XMID.F	0.25	0.040	*
TOL_MGR.H	(-)XMID.H	0.10	0.428	
TOL_MGR.H	(-)TOL_XMID.F	0.12	0.321	
TOL_MGR.H	(-)TOL_XMID.H	0.00	0.971	
NLEA.C	NLEA.F	0.92	0.000	*
NLEA.C	NLEA.H	0.93	0.000	*
NLEA.C	RESmT1.C	0.29	0.016	*
NLEA.C	RESmT2.C	0.30	0.013	*
NLEA.C	RESmT2.F	0.13	0.303	
NLEA.C	RESpT1.C	0.09	0.475	
NLEA.C	RESpT2.C	-0.03	0.797	
NLEA.C	RESpT2.H	-0.04	0.767	
NLEA.C	SLA.C	-0.10	0.429	
NLEA.C	SLA.F	0.25	0.036	*
NLEA.C	SLA.H	0.35	0.003	*
NLEA.C	TGER.C	-0.37	0.002	*
NLEA.C	(-)XMID.C	-0.38	0.001	*
NLEA.C	(-)XMID.F	-0.15	0.210	
NLEA.C	(-)XMID.H	0.20	0.105	
NLEA.C	(-)TOL_XMID.F	0.11	0.376	

trait_1	trait_2	corr. coeff	*p-value*	
NLEA.C	(-)TOL_XMID.H	-0.03	0.798	
NLEA.F	NLEA.H	0.86	0.000	*
NLEA.F	RESmT1.C	0.38	0.001	*
NLEA.F	RESmT2.C	0.23	0.061	
NLEA.F	RESmT2.F	0.10	0.392	
NLEA.F	RESpT1.C	-0.02	0.900	
NLEA.F	RESpT2.C	0.06	0.635	
NLEA.F	RESpT2.H	-0.10	0.432	
NLEA.F	SLA.C	-0.18	0.130	
NLEA.F	SLA.F	0.05	0.683	
NLEA.F	SLA.H	0.24	0.051	
NLEA.F	TGER.C	-0.36	0.003	*
NLEA.F	(-)XMID.C	-0.43	0.000	*
NLEA.F	(-)XMID.F	-0.21	0.081	
NLEA.F	(-)XMID.H	0.11	0.357	
NLEA.F	(-)TOL_XMID.F	0.09	0.449	
NLEA.F	(-)TOL_XMID.H	0.10	0.428	
NLEA.H	RESmT1.C	0.30	0.012	*
NLEA.H	RESmT2.C	0.28	0.022	*
NLEA.H	RESmT2.F	0.12	0.307	
NLEA.H	RESpT1.C	0.09	0.463	
NLEA.H	RESpT2.C	0.09	0.475	
NLEA.H	RESpT2.H	0.07	0.584	
NLEA.H	SLA.C	-0.07	0.575	
NLEA.H	SLA.F	0.16	0.184	
NLEA.H	SLA.H	0.27	0.025	*
NLEA.H	TGER.C	-0.30	0.012	*
NLEA.H	(-)XMID.C	-0.39	0.001	*
NLEA.H	(-)XMID.F	-0.26	0.031	*
NLEA.H	(-)XMID.H	0.26	0.033	*
NLEA.H	(-)TOL_XMID.F	0.00	0.987	
NLEA.H	(-)TOL_XMID.H	0.00	0.977	
RESmT1.C	RESmT2.C	0.27	0.022	*
RESmT1.C	RESmT2.F	0.12	0.334	
RESmT1.C	RESpT1.C	0.35	0.004	*
RESmT1.C	RESpT2.C	0.12	0.326	
RESmT1.C	RESpT2.H	-0.12	0.328	
RESmT1.C	SLA.C	-0.33	0.006	*
RESmT1.C	SLA.F	-0.07	0.556	
RESmT1.C	SLA.H	0.17	0.163	
RESmT1.C	TGER.C	-0.38	0.001	*
RESmT1.C	(-)XMID.C	-0.11	0.382	
RESmT1.C	(-)XMID.F	-0.25	0.039	*
RESmT1.C	(-)XMID.H	0.36	0.003	*
RESmT1.C	(-)TOL_XMID.F	-0.15	0.206	
RESmT1.C	(-)TOL_XMID.H	0.11	0.379	
RESmT2.C	RESmT2.F	0.27	0.025	*
RESmT2.C	RESpT1.C	0.61	0.000	*
RESmT2.C	RESpT2.C	0.09	0.474	
RESmT2.C	RESpT2.H	0.35	0.004	*
RESmT2.C	SLA.C	-0.29	0.017	*
RESmT2.C	SLA.F	0.39	0.001	*
RESmT2.C	SLA.H	0.27	0.024	*
RESmT2.C	TGER.C	-0.33	0.005	*
RESmT2.C	(-)XMID.C	-0.07	0.579	
RESmT2.C	(-)XMID.F	-0.09	0.468	
RESmT2.C	(-)XMID.H	0.29	0.017	*
RESmT2.C	(-)TOL_XMID.F	0.01	0.924	
RESmT2.C	(-)TOL_XMID.H	-0.11	0.377	
RESmT2.F	RESpT1.C	0.22	0.067	
RESmT2.F	RESpT2.C	0.06	0.642	
RESmT2.F	RESpT2.H	-0.02	0.896	
RESmT2.F	SLA.C	-0.30	0.012	*
RESmT2.F	SLA.F	0.16	0.202	
RESmT2.F	SLA.H	-0.16	0.198	

trait_1	trait_2	corr. coeff	*p-value*	
RESmT2.F	TGER.C	-0.23	0.059	
RESmT2.F	(-)XMID.C	-0.17	0.152	
RESmT2.F	(-)XMID.F	0.09	0.487	
RESmT2.F	(-)XMID.H	0.26	0.031	*
RESmT2.F	(-)TOL_XMID.F	0.14	0.248	
RESmT2.F	(-)TOL_XMID.H	0.10	0.404	
RESpT1.C	RESpT2.C	0.01	0.934	
RESpT1.C	RESpT2.H	0.29	0.016	*
RESpT1.C	SLA.C	-0.43	0.000	*
RESpT1.C	SLA.F	0.53	0.000	*
RESpT1.C	SLA.H	0.25	0.039	*
RESpT1.C	TGER.C	-0.23	0.056	
RESpT1.C	(-)XMID.C	0.18	0.145	
RESpT1.C	(-)XMID.F	-0.10	0.413	
RESpT1.C	(-)XMID.H	0.35	0.004	*
RESpT1.C	(-)TOL_XMID.F	-0.14	0.240	
RESpT1.C	(-)TOL_XMID.H	-0.18	0.137	
RESpT2.C	RESpT2.H	0.53	0.000	*
RESpT2.C	SLA.C	-0.10	0.402	
RESpT2.C	SLA.F	-0.23	0.056	
RESpT2.C	SLA.H	-0.13	0.296	
RESpT2.C	TGER.C	-0.26	0.029	*
RESpT2.C	(-)XMID.C	0.08	0.539	
RESpT2.C	(-)XMID.F	-0.14	0.245	
RESpT2.C	(-)XMID.H	0.30	0.013	*
RESpT2.C	(-)TOL_XMID.F	-0.17	0.159	
RESpT2.C	(-)TOL_XMID.H	0.25	0.040	*
RESpT2.H	SLA.C	-0.05	0.713	
RESpT2.H	SLA.F	0.07	0.546	
RESpT2.H	SLA.H	0.12	0.314	
RESpT2.H	TGER.C	0.00	0.985	
RESpT2.H	(-)XMID.C	0.03	0.787	
RESpT2.H	(-)XMID.F	-0.20	0.101	
RESpT2.H	(-)XMID.H	0.23	0.054	
RESpT2.H	(-)TOL_XMID.F	-0.16	0.177	
RESpT2.H	(-)TOL_XMID.H	0.06	0.645	
SLA.C	SLA.F	0.12	0.328	
SLA.C	SLA.H	0.36	0.002	*
SLA.C	TGER.C	0.41	0.000	*
SLA.C	(-)XMID.C	0.19	0.127	
SLA.C	(-)XMID.F	-0.02	0.843	
SLA.C	(-)XMID.H	0.00	0.983	
SLA.C	(-)TOL_XMID.F	-0.13	0.297	
SLA.C	(-)TOL_XMID.H	0.10	0.419	
SLA.F	SLA.H	0.50	0.000	*
SLA.F	TGER.C	-0.09	0.479	
SLA.F	(-)XMID.C	-0.06	0.634	
SLA.F	(-)XMID.F	0.21	0.081	
SLA.F	(-)XMID.H	0.26	0.034	*
SLA.F	(-)TOL_XMID.F	0.23	0.058	
SLA.F	(-)TOL_XMID.H	-0.08	0.493	
SLA.H	TGER.C	0.01	0.960	
SLA.H	(-)XMID.C	-0.01	0.962	
SLA.H	(-)XMID.F	-0.18	0.144	
SLA.H	(-)XMID.H	0.22	0.069	
SLA.H	(-)TOL_XMID.F	-0.08	0.511	
SLA.H	(-)TOL_XMID.H	-0.26	0.030	*
TGER.C	(-)XMID.C	0.10	0.403	
TGER.C	(-)XMID.F	-0.23	0.063	
TGER.C	(-)XMID.H	-0.50	0.000	*
TGER.C	(-)TOL_XMID.F	-0.20	0.107	
TGER.C	(-)TOL_XMID.H	-0.18	0.136	
(-)XMID.C	(-)XMID.F	0.00	0.978	
(-)XMID.C	(-)XMID.H	0.11	0.361	
(-)XMID.C	(-)TOL_XMID.F	-0.60	0.000	*

trait_1	trait_2	corr. coeff	*p-value*	
(-)XMID.C	(-)TOL_XMID.H	-0.12	0.332	
(-)XMID.F	(-)XMID.H	-0.05	0.668	
(-)XMID.F	(-)TOL_XMID.F	0.77	0.000	*
(-)XMID.F	(-)TOL_XMID.H	0.21	0.088	
(-)XMID.H	(-)TOL_XMID.F	-0.19	0.126	
(-)XMID.H	(-)TOL_XMID.H	0.30	0.012	*
(-)TOL_XMID.F	(-)TOL_XMID.H	0.22	0.075	


Pairwise trait correlation based on Pearon's correlation coefficient
SSIZ.C
TGER.C
IGR.F
IGR.C
IGR.H
MGR.F
MGR.C
MGR.H
(−)XMID.F
(−)XMID.C
(−)XMID.H
ASYM.F
ASYM.C
ASYM.H
NLEA.F
NLEA.C
NLEA.H
LA.F
LA.C
LA.H
SLA.F
SLA.C
SLA.H
LDMC.F
LDMC.C
LDMC.H
LTH.F
LTH.C
LTH.H
LDI.F
LDI.C
LDI.H
TOL_IGR.F
(−)TOL_XMID.F
(−)TOL_XMID.H
TOL_ASYM.F
RESmT1.C
RESmT2.F
RESmT2.C
RESpT1.C
RESpT2.C
RESpT2.H
r.corr.coef
0.5
0.0
−0.5
Only correlation with p−value < 0.05 has been shown

Supplementary material - A1 (Chapter 2) : List of species used

List of taxa (species and subspecies) used in the study. Names of species are according to www.infoflora.ch v. 2020, or www.brassibase.cos.uni-heidelberg.de v. 2020. All samples comes from Switzerland, but since mean values across population were used, no information of localities are provided. Associated data reflect the Environmental descriptors described within the method section.

Species name (InfoFlora, 2020)	Species name (BrassiBase, 2020)	IQR_Elev	Med_Elev	Spat_Var.Fl	Spat_Var.Wi	Temp_Var.Fl	Temp_Var.Wi	X.opt	Performance breadth
Alyssoides utriculata		275.987	612.925	3.159	4.060	7.778	9.546	0.506	4.612
Alyssum alyssoides		601.313	893.125	4.124	4.192	9.389	10.082	-1.000	5.832
Alyssum montanum		354.300	653.025	3.686	4.186	8.433	9.342	0.483	1.714
Arabidopsis thaliana		302.575	534.612	4.229	4.084	8.904	9.551	0.879	2.242
Arabis alpina subsp. *alpina*		1314.919	1809.500	7.438	3.288	8.166	8.548	-0.145	2.288
Arabis auriculata		339.925	980.175	3.635	3.738	8.670	9.529	-0.346	2.417
Arabis bellidifolia subsp. *stellulata*	*Arabis stellulata*	634.838	2263.300	4.429	2.315	7.964	8.658	-1.000	7.364
Arabis caerulea		350.650	2639.875	3.063	1.315	7.906	8.181	0.178	4.053
Arabis ciliata		390.162	1471.775	4.730	3.387	8.302	8.849	0.235	5.164
Arabis collina		370.737	515.575	4.443	3.729	9.181	9.524	-1.000	8.386
Arabis nova		598.300	1036.275	4.481	3.956	9.855	10.019	0.017	1.170
Arabis rosea		16.450	479.750	2.968	4.261	7.384	9.843	0.227	4.708
Arabis sagittata		513.100	399.850	4.302	3.659	9.482	8.987	1.000	2.893
Arabis subcoriacea	*Arabis soyeri* subsp. *subcoriacea*	472.425	2121.100	4.176	2.757	7.862	8.384	1.000	7.761
Arabis turrita	*Pseudoturritis turrita*	337.700	649.525	3.957	4.050	8.730	9.322	-0.171	6.962
Aurinia saxatilis		276.387	590.475	3.884	4.200	8.629	9.423	1.000	7.296
Barbarea intermedia		723.100	852.550	4.794	3.551	8.160	9.073	1.000	3.343
Barbarea verna		29.425	427.050	3.919	4.407	9.098	9.832	1.000	3.764
Barbarea vulgaris		395.875	540.700	4.855	4.046	9.518	9.481	1.000	1.984
Berteroa incana		229.325	601.275	2.455	4.365	11.571	10.339	1.000	3.289
Biscutella laevigata		420.750	1797.150	4.926	3.053	8.570	9.317	-1.000	6.814
Camelina microcarpa		450.725	1008.475	4.514	3.855	10.267	10.434	0.392	4.939
Capsella bursa-pastoris		321.063	559.075	3.717	4.100	9.997	9.493	1.000	2.731
Capsella rubella		149.538	465.525	2.811	4.031	10.435	9.353	1.000	5.529
Cardamine alpina		456.962	2489.713	3.799	1.783	7.100	8.054	-0.112	2.501
Cardamine hirsuta		222.862	542.350	3.170	4.244	7.516	9.561	-1.000	3.691
Cardamine impatiens		386.587	565.450	4.450	4.079	9.515	9.453	1.000	24.357
Cardamine resedifolia		702.537	2359.675	4.540	2.525	7.576	8.432	0.810	9.413
Cardaminopsis arenosa subsp. *arenosa*	*Arabidopsis arenosa* subsp.*arenosa*	493.925	706.275	3.988	4.185	9.945	9.572	1.000	2.927
Cardaminopsis arenosa subsp. *borbasii*	*Arabidopsis arenosa* subsp. *borbasii*	309.775	596.613	3.405	4.252	9.951	9.585	-1.000	17.852
Cardaminopsis halleri	*Arabidopsis halleri*	823.656	1141.188	6.390	3.732	9.325	9.675	0.800	4.899
Cardaria draba	*Lepidium draba*	158.269	471.913	4.313	4.264	9.858	9.513	1.000	4.697
Cochlearia pyrenaica		388.613	1360.675	3.416	3.396	9.037	8.995	-1.000	10.872
Descurainia sophia		844.562	1027.650	4.590	3.889	10.635	10.326	-1.000	12.972
Diplotaxis tenuifolia		159.575	448.975	3.301	4.206	10.438	9.704	1.000	5.305
Draba aizoides		1008.369	2237.087	4.900	2.673	7.136	8.281	0.067	4.735
Draba dubia		825.188	2440.188	4.358	2.629	7.854	8.161	1.000	4.903
Draba fladnizensis		395.313	2804.138	3.083	1.411	7.629	7.943	0.013	4.730
Draba hoppeana		284.294	2844.788	2.882	1.338	7.948	8.676	-0.117	6.666
Draba muralis	*Drabella muralis*	224.687	496.625	3.818	4.101	8.833	9.595	0.252	4.142
Draba nemorosa		335.238	1451.350	4.430	3.361	10.145	10.532	1.000	2.635
Draba siliquosa		595.481	2567.875	3.364	1.565	7.850	8.177	-0.062	5.743
Draba tomentosa		674.650	2170.625	3.946	2.868	8.039	7.991	0.016	3.190
Erophila verna	*Draba verna*	257.125	548.075	3.242	4.136	7.409	9.447	-1.000	2.005
Erucastrum gallicum		129.881	445.000	3.256	4.359	7.681	9.871	-1.000	NA
Erucastrum nasturtiifolium		612.550	649.925	5.117	3.623	9.761	9.690	1.000	2.288
Erysimum cheiri		120.969	479.712	3.842	4.253	8.846	9.608	-0.629	5.136
Erysimum rhaeticum		766.169	1353.400	5.686	3.688	9.894	9.828	0.328	3.711
Hugueninia tanacetifolia	*Descurainia tanacetifolia*	119.638	1996.712	3.535	2.788	7.564	8.153	-1.000	4.139
Isatis tinctoria		226.119	495.438	3.956	4.283	9.554	10.174	0.331	9.463
Kernera saxatilis		735.000	1550.350	5.440	3.168	8.067	8.604	1.000	4.109
Lepidium campestre		223.050	467.500	3.934	4.177	8.795	9.468	1.000	4.589
Lepidium virginicum		132.137	417.950	3.293	4.144	10.316	9.534	1.000	4.486
Murbeckiella pinnatifida		246.675	2568.650	2.899	1.231	6.209	6.297	0.183	2.229
Nasturtium officinale		144.213	456.225	2.254	4.404	10.689	9.799	1.000	3.895
Petrocallis pyrenaica		247.525	2078.275	3.341	2.527	7.062	7.397	-1.000	73.936
Rorippa islandica		228.756	464.438	2.911	4.225	10.548	9.606	0.431	4.793
Rorippa sylvestris		143.700	437.400	2.526	4.125	10.699	9.550	0.612	2.526
Sinapis arvensis		203.938	470.350	2.509	4.200	10.612	9.462	1.000	5.676
Sisymbrium altissimum		203.938	470.350	3.457	4.200	10.142	9.462	1.000	2.881
Sisymbrium austriacum		775.900	1287.750	5.580	3.958	9.669	9.816	1.000	4.188
Sisymbrium irio		146.650	494.150	4.336	3.855	10.490	10.006	1.000	8.839
Sisymbrium officinale		247.775	503.675	3.404	4.196	10.073	9.436	1.000	2.415
Sisymbrium orientale		193.263	392.525	4.331	4.180	10.274	9.903	0.538	3.463
Sisymbrium strictissimum		349.825	1234.700	3.644	3.537	11.232	11.009	1.000	2.337
Thlaspi arvense		672.019	663.712	4.189	4.013	8.745	9.600	1.000	8.019
Thlaspi brachypetalum	*Noccaea brachypetala*	479.275	1104.075	4.454	3.261	9.392	10.008	-1.000	7.283
Thlaspi caerulescens	*Noccaea caerulescens*	357.400	1171.125	3.870	3.613	7.942	8.854	1.000	2.201
Thlaspi perfoliatum	*Microthlaspi perfoliatum*	310.981	584.737	3.898	4.227	8.698	9.539	-0.047	1.494
Thlaspi rotundifolium subsp. *corymbosum*	*Noccaea corymbosa*	194.875	2747.900	3.779	1.078	6.608	7.693	-0.008	4.378
Thlaspi rotundifolium subsp. *rotundifolium*	*Noccaea rotundifolia*	465.088	2264.250	3.539	1.999	7.021	7.535	0.066	2.448
Thlaspi sylvium	*Noccaea sylvia*	200.700	2528.500	3.744	1.124	7.298	8.127	0.537	2.214
Turritis glabra		795.494	785.350	4.936	3.959	9.782	9.895	1.000	9.145

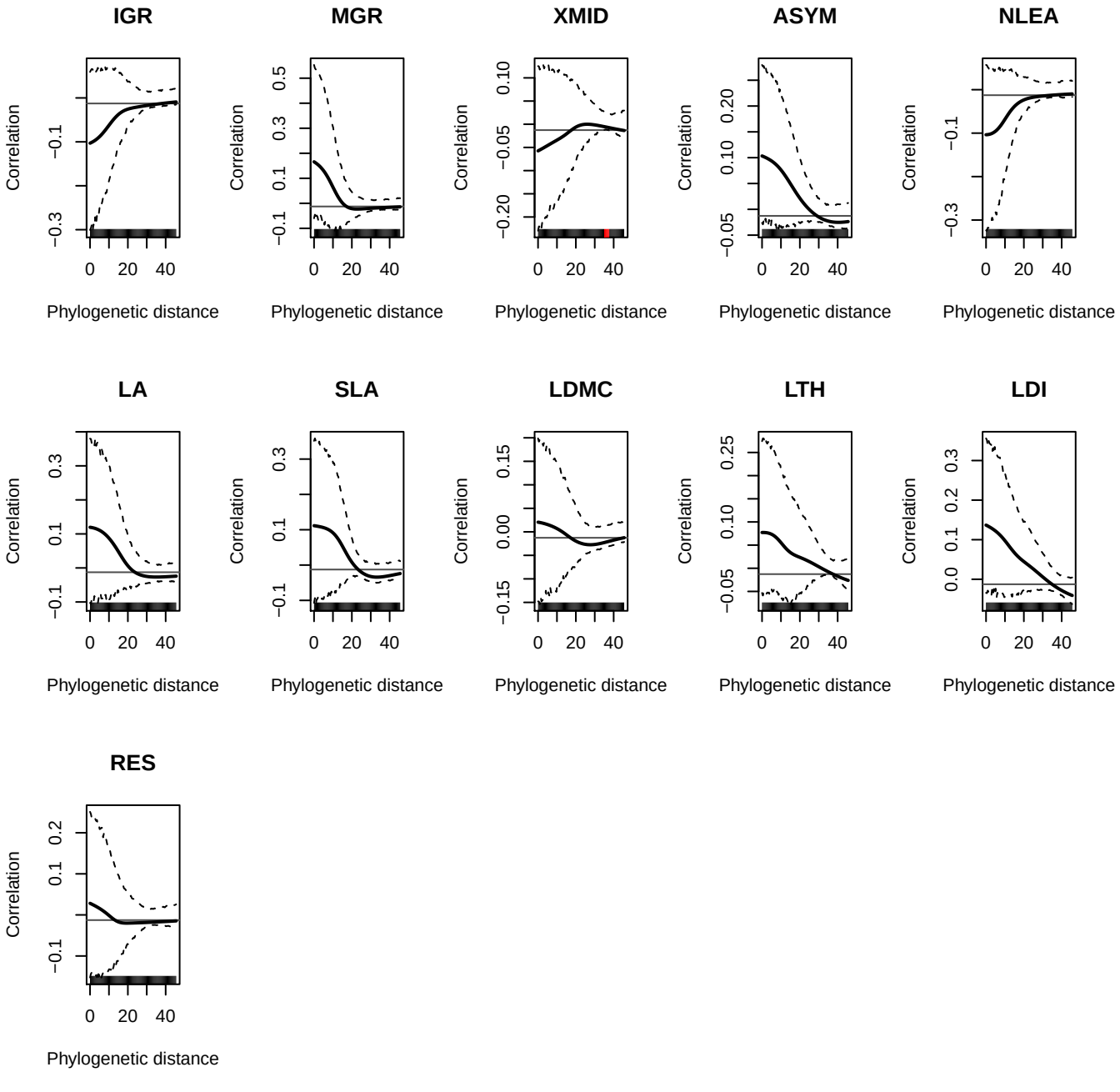
Suppelementary material - A2 (Chapter 2): phylogenetic signal and phylogenetic correlograms

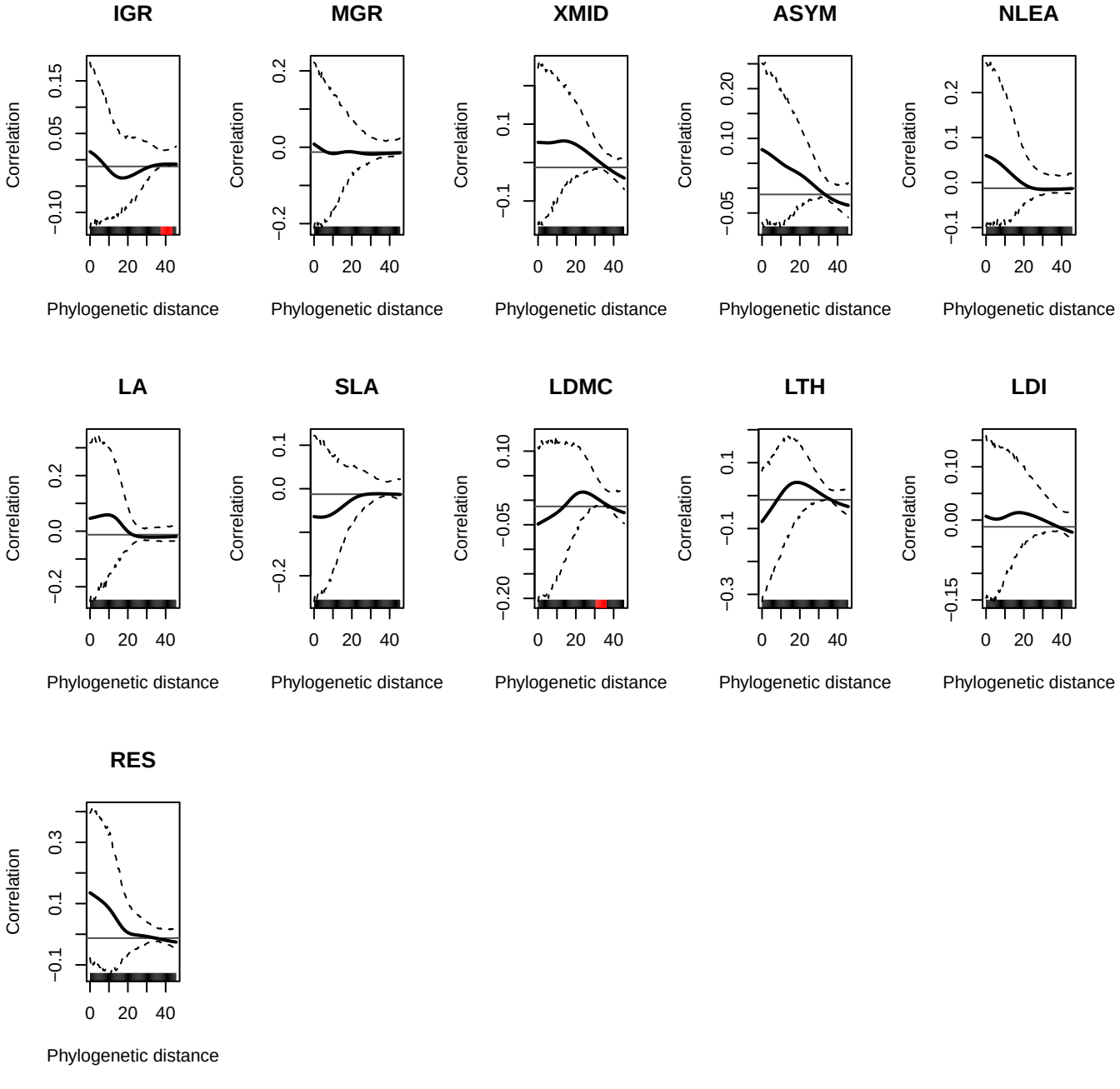
Phylogenetic signal in traits elasticity across multiple environments. Analyses were performed with phylosignal package and significance based on 10'000 permutations. For details refer to method section.

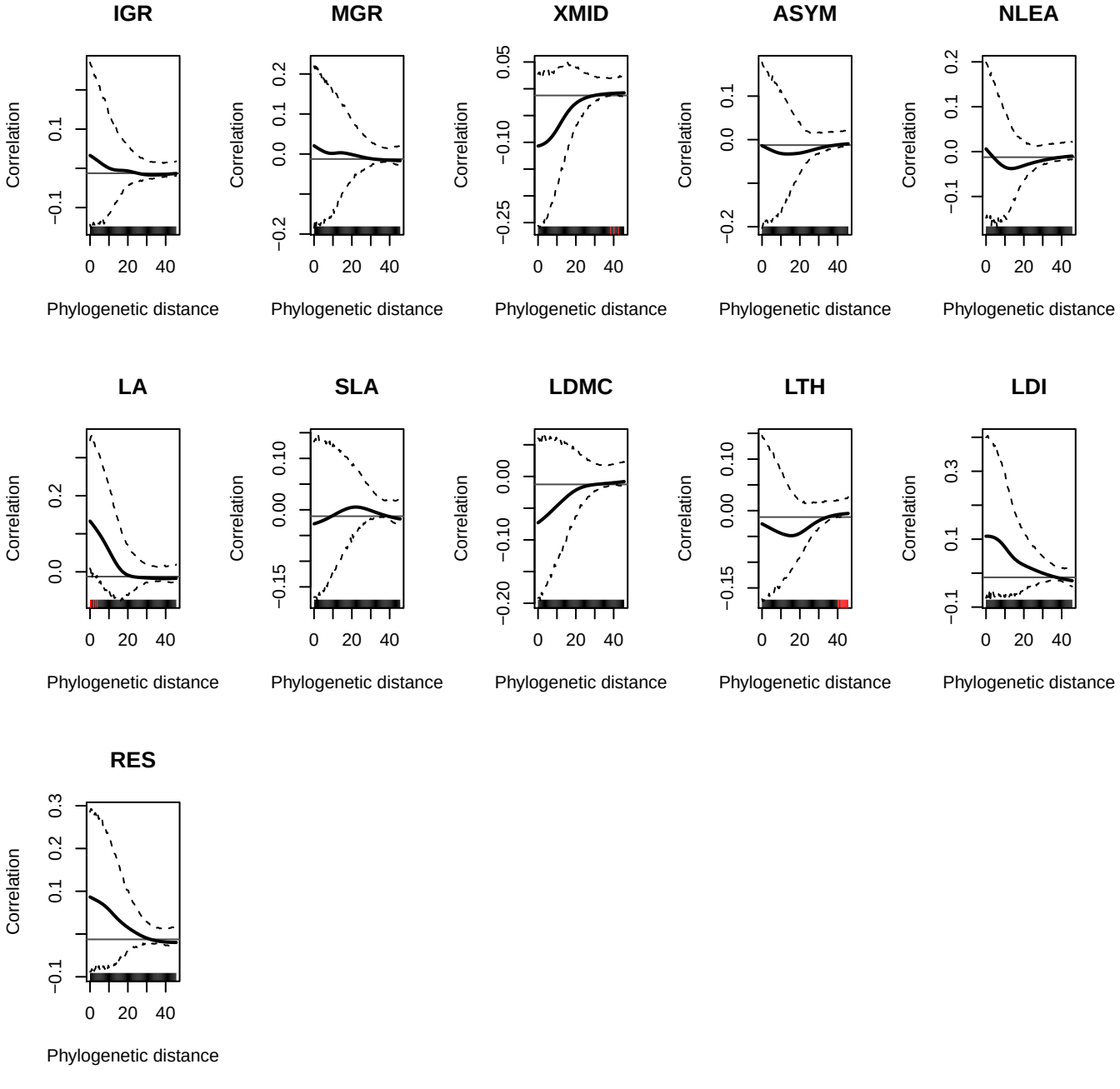
Following pages report phylogenetic correlograms of environmental descriptors, thermal performance and traits elasticity. Significance is based on 95% confidence interval

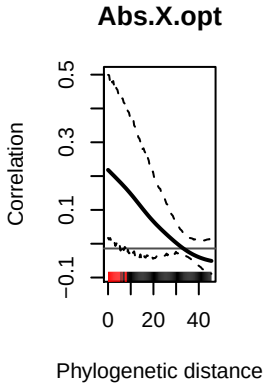
	Moran's *I*	Bloomberg's *K*	Pagel's λ
Elasticity (mild - frost)			
Initial growth rate	-0.037	0.060	0.000
Maximal growth rate	0.021	0.104	0.001
Time of maximal growth rat	-0.047	0.068	0.000
Leaf area	0.036 (.)	0.119	0.185
Specific leaf area	**0.052 ***	0.127	0.212 (.)
Leaf dry-matter content	0.004	0.068	0.000
Leaf thickness	-0.005	0.136	0.060
Leaf dissection index	**0.047 ***	0.124	**0.344 ***
Leaf thermal resistance	0.022	0.125	0.000
Elasticity (mild - heat)			
Initial growth rate	-0.007	0.132	0.000
Maximal growth rate	0.033 (.)	**0.172 ***	0.007
Time of maximal growth rat	0.010	0.088	0.135 (.)
Leaf area	0.022 (.)	0.097	0.169
Specific leaf area	0.008	0.128	0.000
Leaf dry-matter content	-0.019	0.082	0.030
Leaf thickness	-0.029	0.112	0.068
Leaf dissection index	0.006	0.173	0.102
Leaf thermal resistance	**0.072 ****	**0.207 ***	0.222
Elasticity (frost - heat)			
Initial growth rate	-0.015	0.127	0.000
Maximal growth rate	0.039 (.)	**0.168 ***	0.033
Time of maximal growth rat	-0.011	0.112	0.000
Leaf area	0.031 (.)	0.089	0.038
Specific leaf area	-0.036	0.089	0.001
Leaf dry-matter content	-0.056	0.071	0.000
Leaf thickness	-0.023	0.075	0.000
Leaf dissection index	-0.030	0.084	0.170
Leaf thermal resistance	0.031 (.)	0.114	0.148

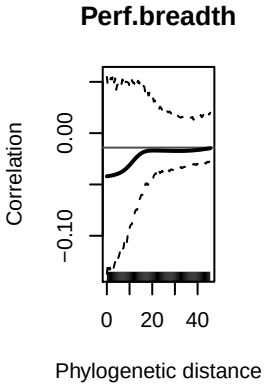
P-values were based on 10'000 permutations. P > 0.1 (.), > 0.05 *, > 0.01 **, > 0.001 ***.
Bold highlight significance

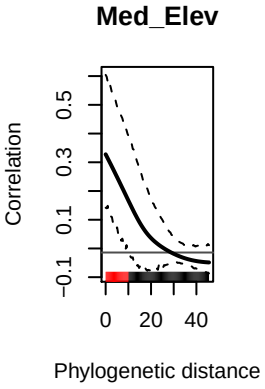

IGR
MGR
XMID
ASYM
NLEA
LA
SLA
LDMC
LTH
LDI
RES
Correlation
Phylogenetic distance
0
20
40

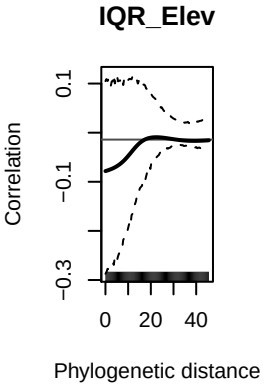

IGR
MGR
XMID
ASYM
NLEA
LA
SLA
LDMC
LTH
LDI
RES
Correlation
Phylogenetic distance
0
20
40

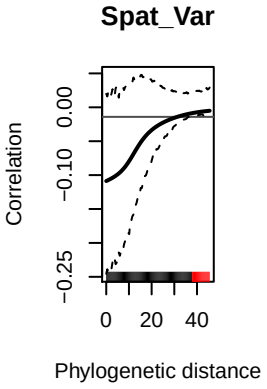

IGR
MGR
XMID
ASYM
NLEA
LA
SLA
LDMC
LTH
LDI
RES
Correlation
Phylogenetic distance
0
20
40

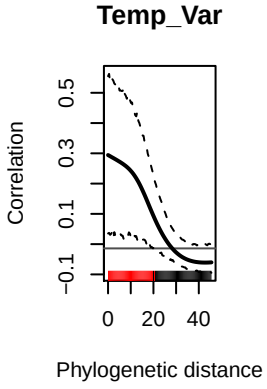

Abs.X.opt
Correlation
0.5
0.3
0.1
−0.1
0
20
40
Phylogenetic distance


Perf.breadth
Correlation
0.00
−0.10
0
20
40
Phylogenetic distance


Med_Elev
Correlation
0.5
0.3
0.1
−0.1
0
20
40
Phylogenetic distance


IQR_Elev
Correlation
0.1
−0.1
−0.3
0
20
40
Phylogenetic distance

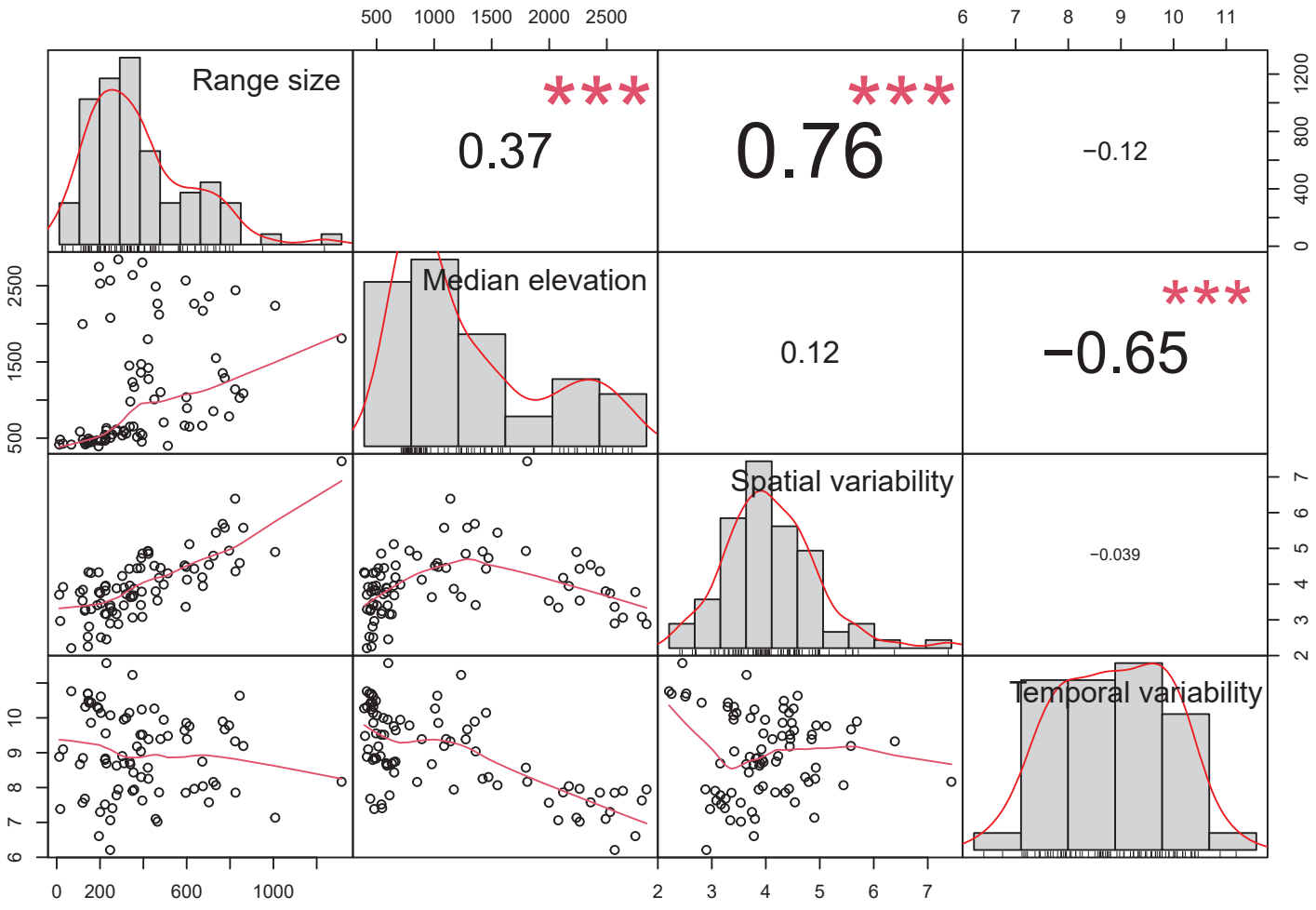

Spat_Var
Correlation
0.00
−0.10
−0.25
0
20
40
Phylogenetic distance


Temp_Var
Correlation
0.5
0.3
0.1
−0.1
0
20
40
Phylogenetic distance

Suppelementary material (A4): correlation matrix

Correlation matrix between the untransformed geographic (range size, i.e. IQR_Elev) and climatic variables (Spatial and temporal thermal variability) used in the study.The median elevation was included as reference.

Each point refers to a species



Supplementary material - A1 (Chapter 3 and Chapter 4): List of species used

List of taxa (species and subspecies) used in the study. Names of species are according to www.infoflora.ch v. 2020, or www.brassibase.cos.uni-heidelberg.de v. 2020. ISFS is the species code used in Infoflora database. Information on the sampling sites includes: the locality with the abbreviation for Canton, the coordinates (X, Y, CH1903 / LV03), the elevation (m asl), the date of sampling, the internal code (sample_ID, University **of Basel, Plant Ecology and Evolutionary group**), the round of sowing plant material was assessed, and the predominant elevational distriubtion of the species, based on Flora Alpina (Aeschimann et al., 2004).

ISFS	Species name (InfoFlora, 2020)	Species name (BrassiBase, 2020)	Locality (Canton)	CoordinateCH_X	CoordinateCH_Y	Elevation	Sampling date	Sample ID
39200	*Arabidopsis thaliana*		Buseno (GR)	728849	125853	660	05.06.2016	0028
39200	*Arabidopsis thaliana*		Basel (BS)	611323	270231	250	10.05.2017	0209
39400	*Arabis alpina* subsp. *alpina*		Medels (GR)	704617	159917	1940	10.08.2016	0103
39400	*Arabis alpina* subsp. *alpina*		Wildhaus Alt St. Johann (SG)	745411	234162	1995	15.09.2016	0151
39800	*Arabis bellidifolia* subsp. *stellulata*	*Arabis stellulata*	Val Müstair (GR)	828677	159977	2860	29.08.2017	0228
39800	*Arabis bellidifolia* subsp. *stellulata*	*Arabis stellulata*	Obergoms (VS)	672460	147169	2300	28.09.2017	0237
40000	*Arabis caerulea*		Zermatt (VS)	628345	96957	2950	13.09.2016	0147
40000	*Arabis caerulea*		Lischana / Scuol (GR)	821865	182995	2670	19.09.2016	0162
40200	*Arabis ciliata*		Zermatt (VS)	627610	95860	2530	27.08.2016	0144
40200	*Arabis ciliata*		Capriasca (TI)	717931	106862	975	12.06.2017	0211
40300	*Arabis collina*		Pazzallo (TI)	716881	92806	900	10.07.2017	0215
41100	*Arabis nova*		Grächen (VS)	629868	115937	1515	15.07.2016	0094
41100	*Arabis nova*		Poschiavo (GR)	802776	132669	1110	20.07.2016	0111
41600	*Arabis sagittata*		Rovio (TI)	720922	88939	775	09.07.2015	0016
41600	*Arabis sagittata*		Montcherand (VD)	527776	175762	562	28.08.2016	0138
58600	*Barbarea vulgaris*		Mendrisio (TI)	721454	85770	1260	09.08.2016	0102
58600	*Barbarea vulgaris*		Hauterive (FR)	575744	179966	470	23.07.2016	0125
77900	*Capsella bursa-pastoris*		Pambio-Noranco (Lugano) (TI)	715433	93240	300	05.05.2016	0026
77900	*Capsella bursa-pastoris*		Pfungen (ZH)	689611	263695	380	09.06.2016	0055
78000	*Capsella rubella*		Melano (TI)	719561	87042	275	27.05.2016	0027
78000	*Capsella rubella*		Fribourg (FR)	578511	184861	600	15.05.2016	0030
78200	*Cardamine alpina*		Poschiavo (GR)	799654	141514	2270	02.09.2016	0119
78200	*Cardamine alpina*		Bedretto (TI)	673084	147930	2500	28.09.2017	0239
78900	*Cardamine hirsuta*		Neuchâtel (NE)	561595	205520	540	28.04.2015	0001
78900	*Cardamine hirsuta*		Zug (ZG)	679912	225784	415	05.05.2015	0002
79000	*Cardamine impatiens*		Neunkirch (SH)	679282	280541	525	03.07.2016	0057
79000	*Cardamine impatiens*		Castel San Pietro (TI)	722528	79912	400	03.06.2017	0207
80300	*Cardamine resedifolia*		Zermatt (VS)	629656	95873	2665	06.08.2016	0095
80300	*Cardamine resedifolia*		Poschiavo (GR)	797461	142862	2245	05.08.2016	0113
80700	*Cardaminopsis arenosa* subsp. *arenosa*	*Arabidopsis arenosa* subsp. *arenosa*	Fribourg (FR)	578953	183152	560	16.06.2015	0006
80700	*Cardaminopsis arenosa* subsp. *arenosa*	*Arabidopsis arenosa* subsp. *arenosa*	Airolo (TI)	691068	153647	1130	29.06.2015	0013
81000	*Cardaminopsis halleri*	*Arabidopsis halleri*	Beride (TI)	708081	95566	484	12.06.2016	0044
81000	*Cardaminopsis halleri*	*Arabidopsis halleri*	St. Moritz (GR)	785255	152806	1750	10.08.2016	0115
135200	*Descurainia sophia*		Sion (VS)	593080	118720	490	06.06.2016	0024
135200	*Descurainia sophia*		Äscher Wildkirchli (AI)	749364	238790	1500	11.07.2016	0077
140700	*Draba dubia*		Quinto (TI)	695022	154237	1820	19.07.2016	0075
140700	*Draba dubia*		Zermatt (VS)	626542	92458	3070	14.09.2016	0150
141200	*Draba muralis*	*Drabella muralis*	Maroggia (TI)	718942	88085	279	15.04.2017	0196
141200	*Draba muralis*	*Drabella muralis*	Uster (ZH)	699287	244107	495	21.06.2017	0202
141400	*Draba siliquosa*		Zermatt (VS)	627286	96017	2570	07.08.2016	0081
141400	*Draba siliquosa*		Pontresina (GR)	797531	143496	2235	04.08.2016	0112
156500	*Erophila praecox*	*Draba verna*	Fribourg (FR)	578476	185388	600	17.05.2016	0031
156500	*Erophila praecox*	*Draba verna*	Origlio (TI)	716594	101509	420	21.04.2017	0204
173500	*Fourraea alpina*		Arzo (TI)	717154	82402	607	09.07.2016	0068
173500	*Fourraea alpina*		San Bernardino (GR)	735773	147364	1840	15.08.2017	0221
208700	*Hugueninia tanacetifolia*	*Descurainia tanacetifolia*	Bourg St. Pierre (VS)	579084	79819	2450	04.10.2016	0140
221000	*Kernera saxatilis*		Seewis (GR)	756696	204989	580	04.07.2016	0065
221000	*Kernera saxatilis*		Pazzallo (TI)	716937	92864	913	19.06.2017	0213
327800	*Pritzelago alpina* subsp. *brevicaulis*	*Hornungia alpina* subsp. *brevicaulis*	Zermatt (VS)	626516	92449	3060	28.08.2016	0146
327800	*Pritzelago alpina* subsp. *brevicaulis*	*Hornungia alpina* subsp. *brevicaulis*	Lischana / Scuol (GR)	821861	182962	2680	19.09.2016	0164
418300	*Thlaspi brachypetalum*	*Noccaea brachypetala*	Amsteg (UR)	692138	178151	670	09.06.2015	0005
418300	*Thlaspi brachypetalum*	*Noccaea brachypetala*	Escholzmatt (LU)	636902	196739	1060	20.06.2016	0048
418800	*Thlaspi perfoliatum*	*Microthlaspi perfoliatum*	Ayent (VS)	597489	124557	906	28.04.2016	0021
418800	*Thlaspi perfoliatum*	*Microthlaspi perfoliatum*	Meride (TI)	716550	84397	620	30.04.2017	0205
419200	*Thlaspi rotundifolium* subsp. *corymbosum*	*Noccaea corymbosa*	San Vittore (GR)	725534	128858	2350	14.08.2016	0106
419200	*Thlaspi rotundifolium* subsp. *corymbosum*	*Noccaea corymbosa*	Zermatt (VS)	619070	92681	2945	08.09.2016	0243
431900	*Turritis glabra*		Mont Noble (VS)	600970	115870	1535	19.08.2016	0098
431900	*Turritis glabra*		Tengia (TI)	706887	147659	1127	22.08.2017	0223

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Adaptation to elevation in *Brassicaceae* in central Alps

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n° AVS: 756.2381.7149.43 | born on: 12 JAN 1990 | citizenship: Swiss | driving license: B (since 11. oct. 2010)

EDUCATION

2017 jan. -
Ph.D Plant Ecology and Evolution; Universität Basel (Prof. Y. Willi, yvonne.willi@unibas.ch)

2013 sep. - 2015 feb.
Master ès sciences in Physiologie et Ecologie des Plantes (cum laude); Université de Neuchâtel

- · Génétique écologique et analyse spatiale (Bouzelboudjen, Felber, Parisod)
- · Ecologie évolutive avancée (Benrey, Felber, Parisod, Praz)
- · Sol et Végétation (Gillet, Gobat, Vittoz)
- · Anatomie fonctionnelle des plantes (Vollenweider)

Master thesis (PD. Dr. Jason R. Grant) : Spéciation cryptique de la fougère Botrychium lunaria (L.) Sw. : diversité génétique et structure biogéographique en Europe.

2010-2013
Bachelor ès science en Biologie; Université de Neuchâtel

Publications

Peer-reviewd

Lucek K, Galli A, Gurten S, Hohmann N, Maccagni A, Patsiou T, Willi Y. (2019). Metabarcoding of honey to assess differences in plant-pollinator interactions between urban and non-urban sites. Apidologie 50(3):317-329.

Dauphin B, Farrar D, Maccagni A, Grant JR. (2018). A worldwide molecular phylogeny provides new insight on cryptic diversity within the moonworts (Botrychium s.s., Ophioglossaceae). Systematic Botany 42(4):620-639.

Maccagni A, Parisod C, Grant JR. (2017). Phylogeography of the moonwort fern Botrychium lunaria (L.) Sw. (Ophioglossaceae) based on chloroplast DNA in the Middle- Europen Mountain System. Alpine Botany 127:185-196.

Reviewer for: Genetics (1), PeerJ (1)

Other

Maccagni A, Kessler M. (2018). La face cachée de la lune. FloraCH 8:11-13.

Marazzi B, Mangili S, Maccagni A, Soldati D, Torriani L. (2018). Atti del Congresso internazionale “Botanica Sudalpina” Museo cantonale di storia naturale, Lugano, 18.11. 2017. Bollettino della Società ticinese di scienze naturali. 106:155-158.

Posters

Maccagni A, Sandoz FA, Grant JR. DNA barcoding of horsetails (Equisetum: Equisetaceae) in Switzerland. 6th International Barcode of Life Conference. SwissBOL. Neuchâtel, Switzerland. 31 Oct. 2014.

Talk

Maccagni A, Willi Y. Evolution and constraints of thermal response in Brassicaceae of the central Alps. Population & Evolutionary Ecology, Biology20. Fribourg, Switzerland 06 Feb. 2020.

Grants/Fundings

2014

Fonds des donations (10'496.- CHF); Université de Neuchâtel.

WORK EXPERIENCE

Teaching

2017 jan. –

Assistant, Plant Ecology and Evolution; Universität Basel (contact: Prof. Y. Willi, yvonne.willi@unibas.ch)

Ecology & Conservation Practical, University of Basel, 2017-18 (BSc course)

Co-supervision of (1) MSc student since October 2018: Janisse Deluigi (Herbivory and elevational gradient; project class activity A2, responsible for A192527 - Herbivory Brassicaceae)

2013 - 2015 may

Student assistant; Université de Neuchâtel (contact: PD PhD. Jason Grant, jason.grant@unine.ch)

Botanique générale (Practical, BSc course), Floristique avancée (Excursions, BSc course)

Herbarium (re-ordering of the collection, determination, mounting and numbering)

2011 sep.

Assistant; Liceo Lugano 1 (contact: Luca Paltrinieri, luca.paltrinieri@edu.ti.ch)

Botanical activity in Val Piora (Practical for 4th year classes, OS BIC).

Extra-academic experiences

2018 aug.

Temporary collaborator, Regional Red List, InfoFlora. (contact: PhD. Brigitte Marazzi, brigitte.marazzi@infoflora.ch)

revision of the national red list, specifically for priority species of the Southern Alps

2016 may-aug.

Scientific collaborator; Universität Basel (contact: Prof. Y. Willi, yvonne.willi@unibas.ch)

seeds and tissue collection and species determination of Swiss Brassicaceae, special focus in Southern Alps

2015 jul.-aug.

Internship; Repubblica e Cantone Ticino (contact: Diego Forni, diego.forni@ti.ch)

botanical survey in vineyards and mountain pasture for SPB II contributions

Languages

Italian : native | French: good | English: discrete | German : basic (school knowledges)

Prizes and certificates

2016

Certificate of knowledge in botany - level “600” ("Dryas"); Schweizerische Botanische Gesellschaft (SBG/SBS)

2015

Prix Henri Spinner; Université de Neuchâtel – for the best master thesis in botany in 2015

2012

Certificate of botanical field knowledge – Level 1 ; Schweizerische Botanische Gesellschaft (SBG/SBS)

2011
“Excellent”, 45° national competition - Schweizer Jungend Forsch; Prix Spécial Art (Universität Basel) – for the maturity work (LAM) "Analisi floristica dell'area torbosa del Motto di Ranscea"

Collaborations and miscellaneous

2019 -
Organizing Committee of the second edition of the Conference "Botanica Sudalpina", Lugano, 20-22 Nov. 2020 (botanicasudalpina.ch)

2019 -
Alumni-Leader (region: Ticino), Schweizere Jugend Forscht (SJF)

2018
Organizing Committee of the Symposium "Breakthrough in Plant Science" for the 20th anniversary of the Plant Science Center (PSC) 2018, Zurich, 5 Dec. 2018

2017
Organizing Committee of the first edition of the Conference "Botanica Sudalpina", Lugano, 18 Nov. 2017 (botanicasudalpina.ch)

2016 –
volunteer collaborator of InfoFlora

2012 - 2015
volunteer collaborator of InfoFlora (region South Alps), project “Red List 2011-2015”

Associations

Schweizerische Botanische Gesellschaft (SBG/SBS) | Società Ticinese di Scienze Naturali (STSN) | Societé Systematique Suisse (SSS) | Società Ticinese di Botanica (SBT, founding- and committee member, since 2016) | Farnfreunde der Schweiz (committee member, since 2020)

Interest

Botany | Briology | Hiking | Nature and macro photography

Army

2018 -
ProtezioneCivile - Compagnia 55 (Lugano Città), Ass. Stato Maggiore, Cpl. ANSIT-TM and archivist. With BLS-DAE-SRC.

Lugano, the 02 Mar. 2020